A SYSTEMATIC TREATMENT **OF ACACIA COULTERI** (FABACEAE, MIMOSOIDEAE) AND SIMILAR SPECIES IN THE NEW WORLD¹

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ABSTRACT

Detailed descriptions, habitat preferences, geographic ranges, and representative specimens are given for the 13 taxa of the Acacia coulteri group from Mexico, Central America, and the southwestern United States. These species form a distinct group within Acacia series Vulgares, lacking prickles and usually having persistent stipules. A principal components analysis (PCA) of vegetative and floral features shows that the specimens examined form discrete units in plots of the first three principal components. The groups established by PCA mostly coincide with previously described species. The taxa within this group are phenetically similar, sharing many morphological features. These data also suggest that there is occasional gene flow between species, but that hybrids are not common. About half the species have restricted ranges (A. compacta, A. dolichostachya, A. durangensis, A. millefolia, A. russelliana, A. sericea, and A. willardiana), but the remainder are wide-ranging, either from Oaxaca and Puebla north into central and northern Mexico (A. acatlensis, A. coulteri, A. mammifera, and A. salazari), or south into Central America (A. centralis and A. usumacintensis).

Key words: Acacia coulteri group, Acacia series Vulgares, Fabaceae, phytogeography, principal components analysis, species delineation, hybridization.

Acacia Miller series Vulgares Benth. (Fabaceae: Mimosoideae), consists of about 200 species distributed in tropical and subtropical wet to dry habitats, in both the Old and New Worlds. Series Vulgares broadly corresponds to subgenus Aculeiferum Vassal (1972), according to Pedley (1978). Later, Pedley (1986) suggested that this subgenus should be elevated to generic status under the name Senegalia Raf. More recent systematic studies suggest that Acacia series Vulgares may not represent a monophyletic group (Chappill & Maslin, 1995; Clarke, 1995). Most species of Acacia series Vulgares are of diverse habitat, habit, morphology, and chemistry. Most are shrubs or small trees, though some are tree-lianas, with branches scrambling over other vegetation. Most species are armed with prickles on the stems, leaf petioles, and rachises. Leaves are bipinnately compound with deciduous stipules, and

numerous pairs of pinnae and leaflets. Peduncles are solitary, or in racemose clusters, from the leaf axils, and flowers form globose heads or cylindrical spikes. Legumes of series Vulgares are relatively large, strongly flattened, usually dehiscent, and with a single row of relatively large seeds. This series is often separated from two other Acacia series, Gummiferae and Filicinae, by the presence of prickles that are scattered along the stems and sometimes the leaf rachises (Bentham, 1875). Acacia series Vulgares can be divided into several informal "species groups" based on overall similarities of habit, stipule persistence, the presence or absence of prickles, petiolar gland shape and structure, as well as inflorescence shape. At present, however, these informal groups within the series have not been established to be monophyletic units. The taxa of one of these groups of phenetically similar species, "the Acacia coulteri

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group" (Maslin & Stirton, 1997), are erect shrubs or small trees with persistent stipules and flowers in cylindrical spikes. Except for minor differences in flower size and occasionally pubescence, flowers are quite similar, with a tubular calyx and corolla, each 5-lobed, numerous separate stamens, and a short-stalked pistil. The 13 species of the A. coulteri group range from Arizona, south through Mexico into Costa Rica. They are morphologically distinct from other species of Acacia series Vulgares in that they always lack prickles, are never lianas, and by a number of other features. Nonetheless, taxonomic treatments have not dealt with this group as a separate unit within the Acacia series Vulgares (Bentham, 1875; Standley, 1920; Britton & Rose, 1928). Many sterile and fruiting specimens of species of the A. coulteri group have been misidentified, adding to the taxonomic confusion. Flowering specimens of Albizia, Lysiloma, and Piptadenia can easily be distinguished from spicate species discussed in this work. In contrast to the A. coulteri group; Albizia and Lysiloma have capitate inflorescences. Although inflorescences of Piptadenia species are spicate, these flowers have 10 stamens with straplike filaments and oblong anthers that are larger than those of Acacia. Stamen filaments of flowering specimens of Albizia and Lysiloma have stamens of about the same number and size as those in Acacia, but the filaments are united into a distinct tube. Capitate species are normally evident, even in fruiting condition. Most fruiting specimens of Piptadenia can be recognized by stamen remnants at the base of the fruits; its strongly venose fruits appear distinct from those of Acacia species, especially if comparative material is available. Careful search of most Piptadenia specimens reveals the presence of prickles, which are completely absent from all members of the A. coulteri group, as well as from members of the genera Albizia and Lysiloma. Two spicate species of the latter genus, L. acapulcense and L. auritum, are sometimes confused with members of the A. coulteri group. For these two species, the two parallel sutural ribs are fused around the periphery of the pod; these ribs often separate from the valves (Barneby & Grimes, 1996). Vegetative specimens of several Lysiloma species may be confused with Acacia species of this group. Some Lysiloma species have cordate-auriculate stipules (at least on young branches) that are never found on the species treated in this work. Finally, vegetative specimens of Albizia usually can be differentiated by the palmate/pinnate venation present in the leaflets (Barneby & Grimes, 1996). The only other member of Acacia series Vulgares

with which species of the A. coulteri group are easily confused is A. macilenta Rose. Often, herbarium specimens of this last species lack prickles, and those specimens that lack prickles are superficially similar to some members of the A. coulteri group. Their separation is straightforward, however, as A. macilenta has petioles that are consistently less than 25 mm long, and the single petiolar gland is dark brown and shallowly volcano-shaped. In largeleaved species of the A. coulteri group with which A. macilenta might be confused, the petioles exceed 25 mm in length and have petiolar glands that are light green or yellow and not volcano-shaped. Concepts and identification of taxa of the A. coulteri group have been unclear in the past. No functional keys that permit accurate identification of these taxa have been published. Surprisingly, in most herbaria, up to half the specimens of this group of species were misidentified. Further, a cladistic analysis based on molecular data from chloroplast restriction site analyses (Clarke, 1995), and cladistic analyses by Catherine Glass and David S. Seigler based on morphological data (unpublished) suggest a more ancient origin of these taxa than other species of Acacia series Vulgares. Otherwise, there are no comprehensive studies on the phylogenetic relationships of the Acacia coulteri group. The present study was undertaken to clarify the taxonomic status and discreteness of the taxa involved, as well as to provide accurate descriptions of and functional keys to these species.

MATERIALS AND METHODS

About 500 Acacia specimens, obtained from 27 herbaria (A, ARIZ, ASU, BM, BR, CM, DS, EIU, F, G, GH, ILL, ISC, LL, MEXU, MIN, MO, MU, NY, POM, RSA, SD, TEX, UC, US, VT, WIS), were studied to determine the geographic ranges and morphological variation of the species in the A. coulteri group. These specimens were initially separated into groups based on the similarity of morphological characteristics. After removal of duplicate and incomplete specimens, only 15 to 25 specimens of most groups remained available for subsequent analysis. Only unambiguous specimens were scored and are indicated in the exsiccatae by an asterisk. Of the original specimen pool, 237 were scored for 1 floral and 14 vegetative characters (Table 1). All characters were measured for each specimen (three or more measurements) and plotted to confirm that gaps existed in order to permit the use of scored characters. The data were then analyzed by principal components analysis (PCA) using NTSYS-pc version 1.70 (Rohlf, 1993).

Characters scored for the principal compo-Table 1. nent analysis of the 13 species of the Acacia coulteri group.

Table 2. Principal components for the data set for the Acacia coulteri group.

group. 1. Bark of trunk (1 = not exfoliating, 2 = exfoliating). 2. Patiala nubercance (1 = alabraus ar nearly as $2 =$	Character number	Component number		
		1	2	3
2. Petiole pubescence $(1 = \text{glabrous or nearly so}, 2 = \text{ouberulent with appressed hairs}, 3 = woolly pubescent}$.	1	0.704	0.113	0.203
3. Petiole length $(1 = 0-10 \text{ mm}, 2 = >10-99 \text{ mm}, 3$	2	-0.638	-0.033	0.678
= >99 mm).	3	0.698	-0.244	0.008
4. Small purple glands on petiole, rachis, and pinnae	4	-0.651	-0.040	0.526
achises $(1 = absent, 2 = present)$.	5	0.396	0.782	0.250
5. Petiole gland structure $(1 = sessile, 2 = stalked, 3$	6	0.352	0.810	0.435
= absent).	7	-0.446	0.428	-0.272
6. Petiole gland apex $(1 = flattened, 2 = doughnut-$	8	-0.139	0.564	-0.409
haped, $3 = \text{globose}, 4 = \text{absent}$).	9	0.744	-0.144	0.024
7. Rachis length (1 = absent, 2 = 1-20 mm, 3 = >20	10	0.427	-0.444	0.589
nm).	11	-0.280	-0.189	-0.761
8. Number of pinna pairs $(1 = 1 \text{ to } 6, 2 = 7 \text{ or more})$.	12	0.356	-0.368	0.353
9. Petiolule length (1 = ≤ 2.4 mm, 2 = > 2.4 mm).	13	0.469	0.545	-0.188
0. Distance between leaflets $(1 = \le 1.5 \text{ mm}, 2 = >1.5$	14	-0.404	0.394	0.441
nm).	15	-0.773	0.006	0.189
1. Number of leaflet pairs per pinna $(1 = <36, 2 = >36)$.	Percent of variance	28.2	17.9	17.2
2. Leaflet length $(1 = 4-36 \text{ mm}, 2 = >36-65 \text{ mm})$. 3. Leaflet apex $(1 = \text{obtuse to broadly acute}, 2 = \text{nar-}$				

rowly acute to acuminate).

14. Leaflet pubescence (1 = glabrous or nearly so, 2 =pubescent with appressed hairs beneath, 3 = pubescent

tively, or 63% of total variance (Tables 1, 2). The amount of variance contributed by the remaining components diminished slowly from the third principal component onward. The best perspective for display of the phenetic groupings was seen in the ordination based on the second and third principal components (Fig. 1). This figure presents all taxa, clearly resolved in one view. In this plot, 13 distinct groups, corresponding to the 13 previously defined species can be observed, although the data clusters of some groups are proximal. Perianth pubescence, petiolule length, and exfoliating bark (characters 15, 9, 1) were the most important characters for determining the component score for the first principal component axis (Table 1). Petiolar gland apex, petiolar gland structure, and the number of pinna pairs (characters 6, 5, 8) were most important for the second principal component axis. The most important characters for the third principal compo-

with appressed hairs on both surfaces, 4 = long hairs clustered at the base of midrib beneath).

15. Perianth pubescence (1 = glabrous or nearly so, 2 =pubescent with appressed hairs, 3 = woolly pubescent).

Data were transformed by a square root transformation (Sokal & Rohlf, 1969). Groups were analyzed separately, in various combinations, and simultaneously.

Because cyanogenesis has previously been found in many Acacia species, and is sometimes useful taxonomically (Seigler & Ebinger, 1988, 1995; Clarke et al. 1989, 1990), all specimens were tested for the presence of cyanogenic compounds by the Feigl-Anger method (Feigl & Anger, 1966; Tantisewie et al., 1969). Seigler et al. (1978) reported a few herbarium specimens of A. acatlensis that released cyanide, and Conn et al. (1989) reported weakly positive cyanide tests for both A. acatlensis and A. coulteri using fresh, air-dried leaf material. During the present study, no material examined gave a positive-test for cyanide, even after the addition of emulsin.

RESULTS AND DISCUSSION

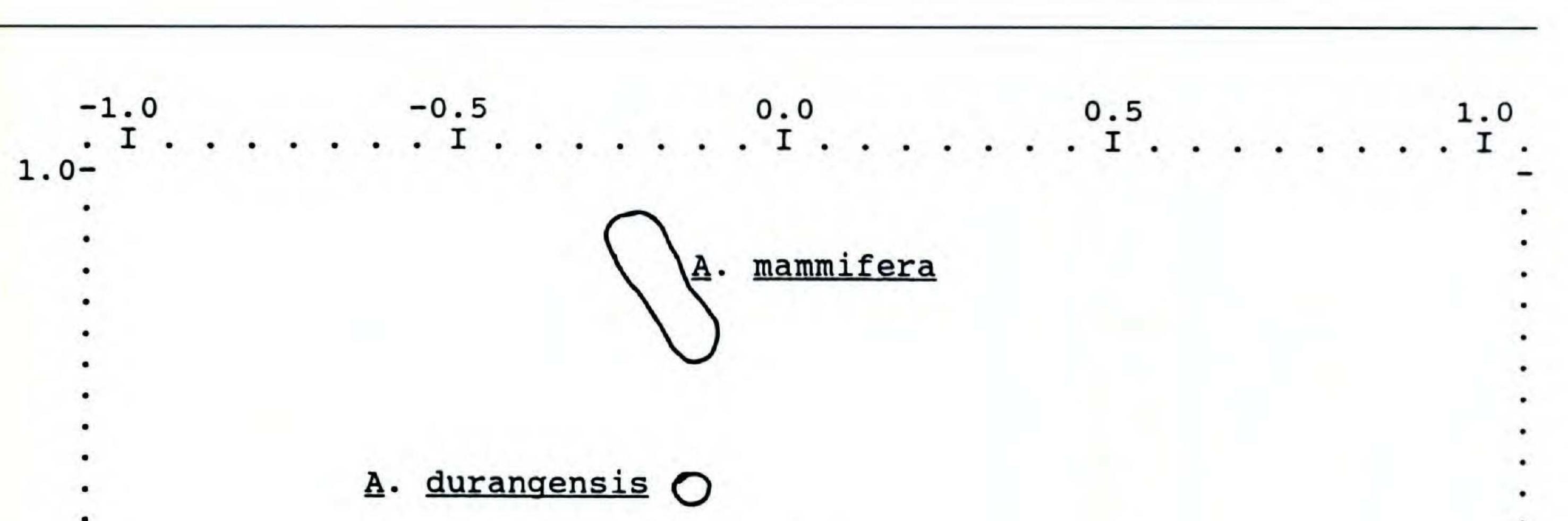
When the entire set of 237 specimens was analyzed using PCA, the first three principal components accounted for 28%, 18%, and 17% respecnent axis were leaflet pairs per pinna, petiole pubescence, and the distance between leaflets (characters 11, 2, 10).

The clusters on this plot do not contain recognizable subgroups, and, except for A. usumacintensis and A. dolichostachya, which nearly overlap on this plot, each of the clusters is clearly separated from the others (Fig. 1). In addition, the OTUs of each group are closely spaced, indicating that the species are homogeneous.

In addition to those herbarium specimens borrowed, the present treatment is also based on extensive collections and observations of these taxa

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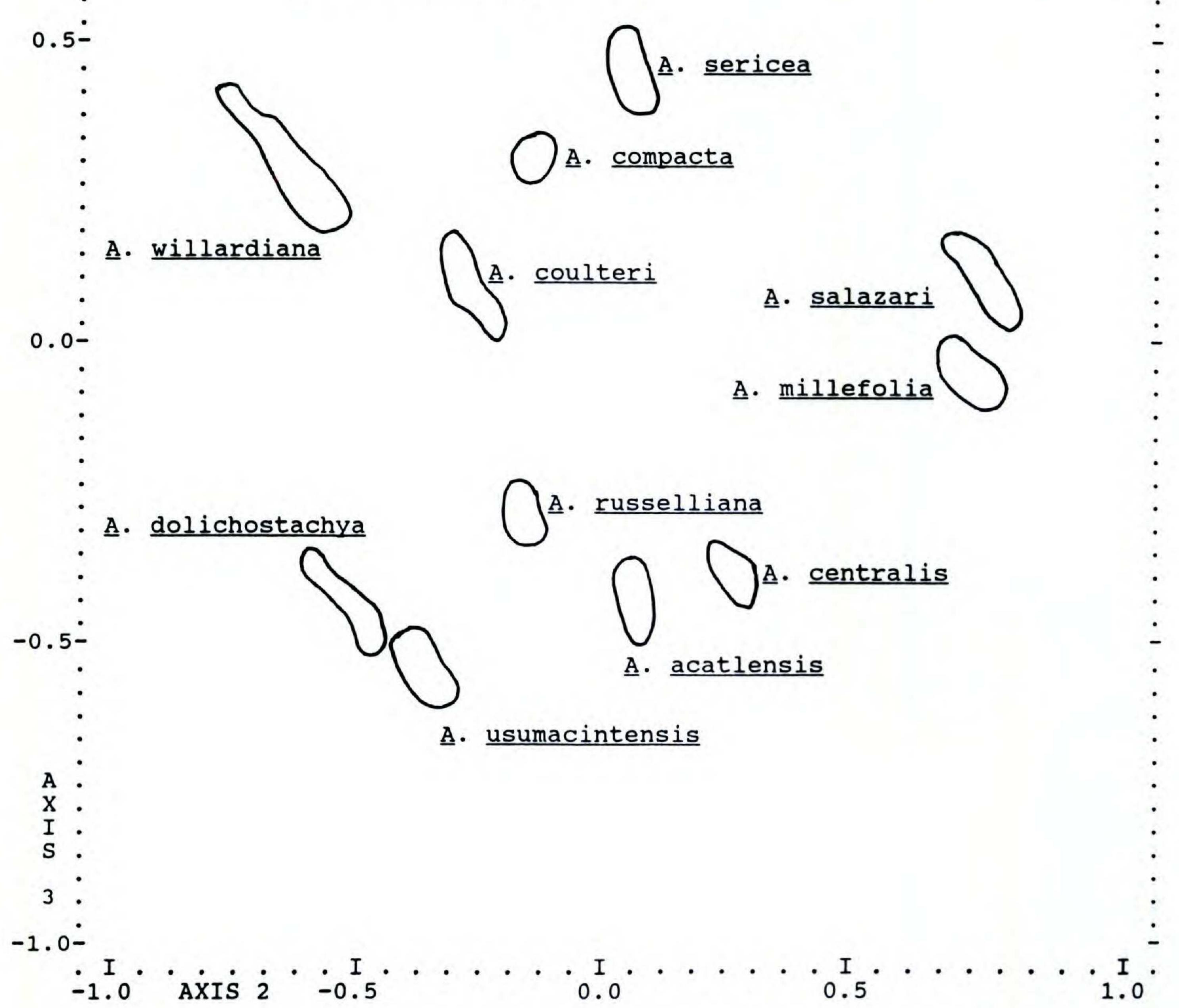


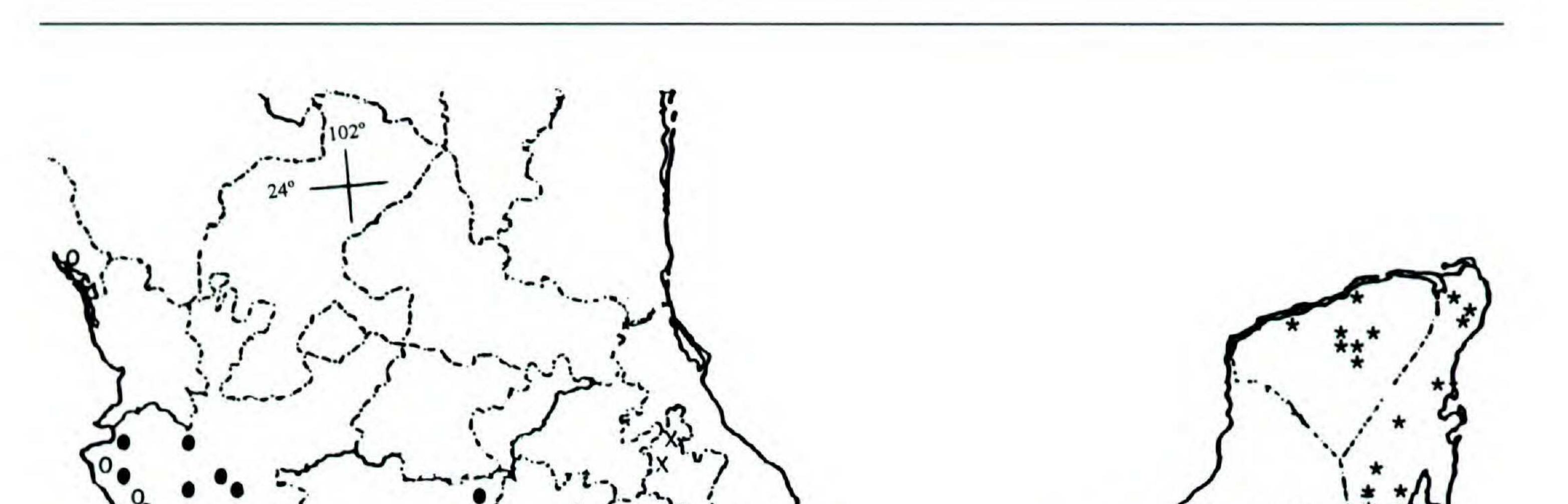
Figure 1. Plot of axis 2 versus 3 of a principal components analysis, using one floral and 14 vegetative variables

from 237 specimens of the Acacia coulteri group.

in Mexico and Central America by one of the authors (DSS) on 15 trips during 1975–1998. Only the most reliable, diagnostic characteristics were used to distinguish the taxa. Although floral characteristics were measured carefully, and are included in the descriptions, flower variation and character overlap precludes using them for distinguishing species. Extensive lists of representative specimens are included, as specimens are commonly misidentified. Also, all specimens used in the PCAs are included in the list of representative specimens (designated by an asterisk after the herbarium abbreviation). Synonyms and types are included, along with maps showing the geographic distribution of each species (Figs. 2, 3).

Occasionally, a few flowering specimens lack leaves, or have extremely small leaves, making it difficult to determine the number of leaflets per pinna and the number of pinnae per leaf. Even with these specimens, the number of pinnae per leaf of532

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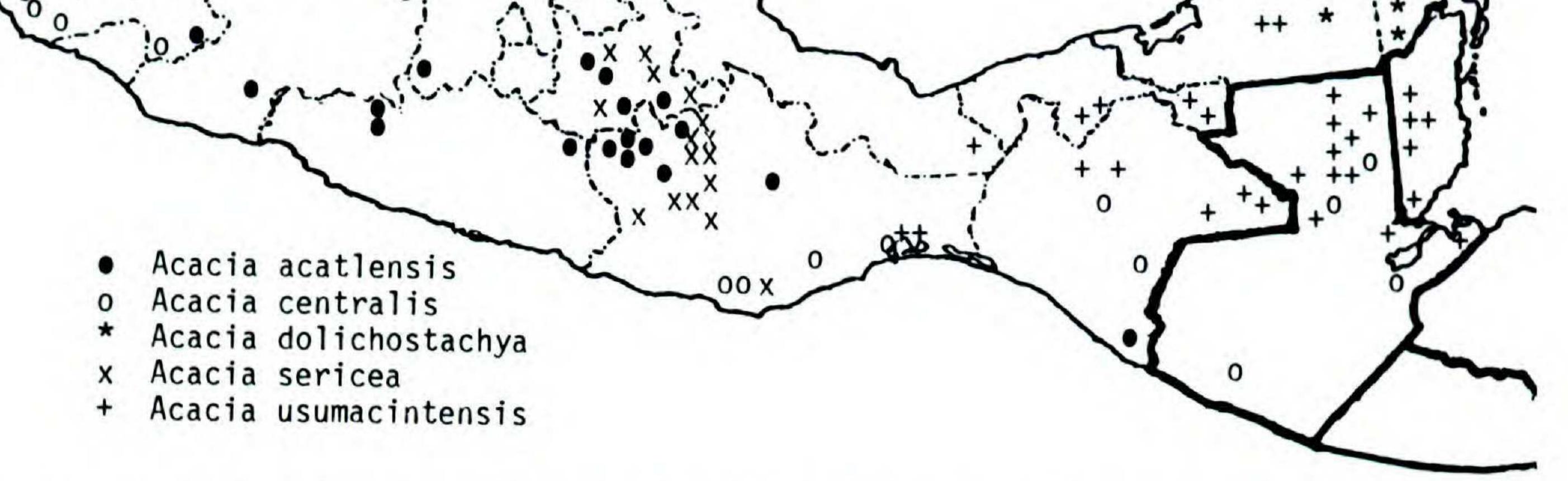


Figure 2. Distribution of Acacia acatlensis, A. centralis, A. dolichostachya, A. sericea, and A. usumacintensis in Mexico, Belize, and Guatemala. The distribution of A. centralis in the rest of Central America is not shown.

ten can be determined from small emerging leaves, are only lightly appressed pubescent, whereas, in or by counting the number of pinna scars on an old the latter, the calyx, corolla, and floral bracts are rachis that may be present. In excess of 500 specdensely sericeous pubescent. Two other species have these small purple glands and occur within imens were examined in this study and few lacked leaves altogether. Most of these were either Acacia the same geographic range. Acacia compacta is a acatlensis or A. sericea. Minute purple glands on small shrub with short shoots, and A. mammifera the young stems and peduncles of both taxa distinis a small tree with flowers that have cream-colored guish them from other members of this group of corollas with a purplish tinge. However, these are species. Acacia acatlensis is then separated from A. only uncommonly found in flowering condition sericea because the former's calyx and floral bracts without leaves.

KEY TO SPECIES

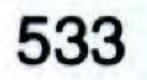
- 1a. Pinnae mostly with more than 36 pairs of leaflets, especially those near the middle of the rachis.
 - 2a. Petiolar gland(s) flattened, usually located on the lower third of the petiole; leaflet apex obtuse to broadly acute.
 - 3a. Leaflets 1.2–1.9 mm wide; leaves with more than 6 pairs of pinnae
 3b. Leaflets mostly less than 1.2 mm wide; most leaves with 6 or fewer pairs of pinnae
 - 2. A. dolichostachya 2b. Petiolar gland(s) saucer-shaped to cup-shaped, usually located on the upper half of the petiole, rarely absent; leaflet apex narrowly acute to acuminate.
 - 4a. Minute purple glands common at the base of the leaflets and usually along the rachis; leaflets lacking long hairs on the lower side at the base
 3. A. acatlensis
 - 4b. Minute purple glands absent; leaflets usually with long hairs on the lower side at the base ------

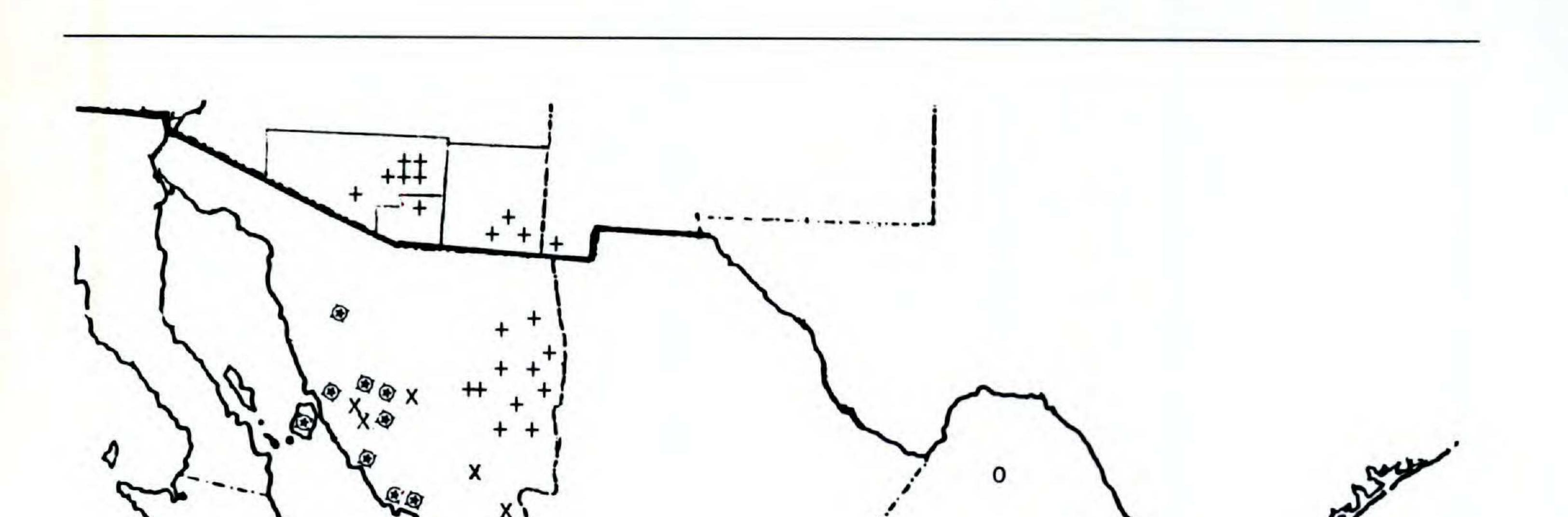
4. A. centralis

1b. Pinnae mostly with fewer than 36 pairs of leaflets, or pinnae absent.

- 5a. Leaves less than 30 mm long, some clustered on short shoots ______ 5. A. compacta
- 5b. Leaves more than 30 mm long; short shoots absent; pinnae sometimes absent in Acacia willardiana.
 - 6a. Leaflets appressed to erect pubescent on both surfaces, usually densely so; minute purple glands common on the rachis and pinna rachises.
 - 7a. Petiole and rachis densely pubescent with erect hairs about 0.3 mm long; petiolules less than 2.1 mm long; fruit pubescent ______6. A. sericea
 - 7b. Petiole and rachis glabrous or with short, appressed hairs; petiolules more than 2.0 mm long; fruit glabrous.

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- Acacia compacta
- Acacia coulteri
- Acacia durangensis A

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- Acacia mammifera *
- Acacia millefolia
- Acacia russelliana X
- Acacia salazari Acacia willardiana ۲



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Figure 3. Distribution of Acacia compacta, A. coulteri, A. durangensis, A. mammifera, A. millefolia, A. russelliana, A. salazari, and A. williardiana in the U.S.A., Mexico, Belize, and Guatemala.

- 8a. Petiolar glands raised, the apex bulbous; most leaves with fewer than 7 pairs of pinnae 7. A. mammifera 8b. Petiolar glands sessile and with an irregularly raised apex; most leaves with more than 10 pairs of pinnae 8. A. durangensis
- 6b. Leaflets glabrous or lightly appressed pubescent beneath; minute purple glands absent.
 - 9a. Leaves mostly with a single pair of pinnae (rarely 2 or 3); many petioles more than 100 mm
 - Leaves mostly with 4 or more pairs of pinnae; petioles less than 70 mm long. 9b. 10a. Rachis gland between the upper pinna pair stalked; shrub or small tree less than 4 m
 - 10b. Rachis gland between the upper pinna pair sessile, usually saucer-shaped, cup-shaped, or absent; large shrub or tree; more than 4 m tall.
 - 11a. Bark of trunk and larger branches exfoliating and papery; petiolar glands absent on many petioles; leaflet apex acuminate _____ 11. A. salazari
 - 11b. Bark of trunk and larger branches smooth to furrowed, not exfoliating; petiolar glands present; leaflet apex broadly acute to obtuse.
 - 12a. Leaflets appressed pubescent beneath; rachis and pinna rachises puberulent above; perianth pubescent 12. A. coulteri
 - 12b. Leaflets glabrous beneath; rachis and pinna rachises as well as perianth glabrous or nearly so ______ 13. A. russelliana

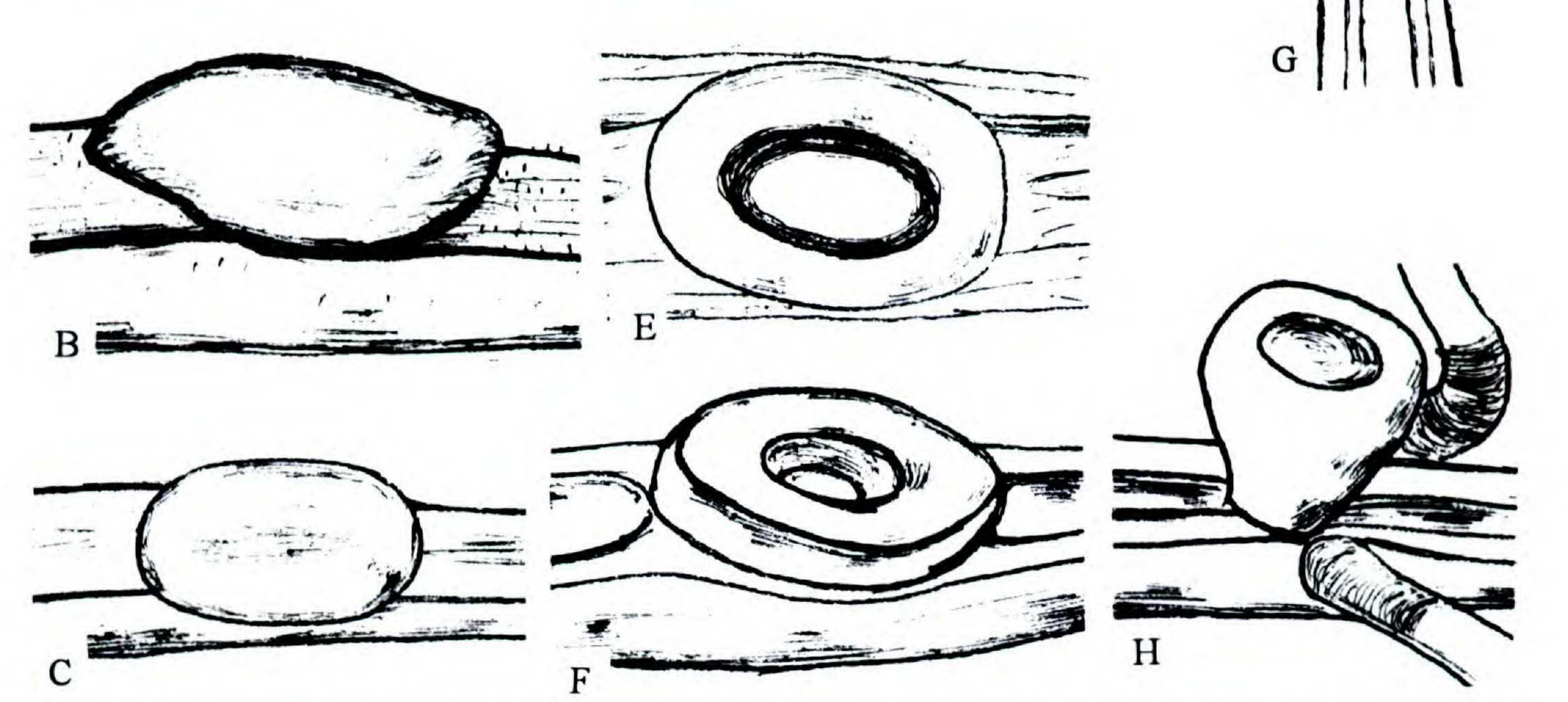


Figure 4. Petiolar glands. —A. Acacia durangensis. —B. A. usumacintensis. —C. A. dolichostachya. —D. A. mammifera. —E. A. coulteri.—F. A. centralis. —G. A. williardiana. —H. A. compacta.

 Acacia usumacintensis Lundell, Contr. Univ. Michigan Herb. 4: 8. 1940. TYPE: Mexico. Tabasco: Boca Cerro on the Río Usumacinta above Tenosique, 1-5 July 1939, E. Matuda 3550 (holotype, MICH!; isotypes, K!, LL!, MEXU!, MICH!, NY!).

Tree to 30 m tall with bark dark gray, shallowly furrowed; twigs brown to greenish brown, not flexuous, glabrous to lightly puberulent; short shoots absent. Leaves alternate, 90–200 mm long; stipules herbaceous, light brown, narrowly triangular, to 2.2 × 0.5 mm near the base, glabrous to lightly puberulent, persistent; petiole adaxially shallowly grooved, 30-70 mm long, glabrous to lightly puberulent; petiolar gland solitary, usually located on the lower third of the petiole, sessile, commonly elliptical, 1-6 mm long, flattened, glabrous (Fig. 4B); rachis adaxially grooved, 50-140 mm long, glabrous to lightly puberulent, a sessile, saucershaped gland, 1.0–1.9 mm across, between the upper pinna pair; pinnae 7 to 15 pairs per leaf, 55-90 mm long, 5–12 mm between pinna pairs; petiolules 1.7-3.0 mm long; leaflets (33)36 to 55 pairs per pinna, opposite, 1.0–1.6 mm between leaf-

lets, oblong, $4-7 \times 1.2-1.9$ mm, glabrous, lateral veins obvious, with a midvein and 1 to 3 smaller veins from the base, base oblique, margins ciliate, apex acute to obtuse. Inflorescence a loosely flowered cylindrical spike 50-110 mm long, 1 to 3 from the leaf axil, or sometimes in terminal racemose clusters; peduncle 7–15 \times 0.7–1.1 mm, puberulent; involucre absent; floral bracts linear, to 1 mm long, puberulent, early deciduous. Flowers sessile, creamy-white; calyx 5-lobed, 1.1-1.5 mm long, densely appressed pubescent; corolla 5-lobed, 1.8-2.5 mm long, densely appressed pubescent; stamen filaments 4-6 mm long; ovary glabrous to lightly pubescent, on a stipe to 0.3 mm long. Legumes light yellowish brown to dark brown, straight, flattened, oblong, 90–250 \times 20–33 mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 22 mm long; apex acute. Seeds uniseriate, no pulp, dark reddish brown, oblong to oval, strongly flattened, 8.8–10.0 \times 7.0–9.0 mm, smooth; pleurogram U-shaped, 3-4 mm across. Flowers: April–June.

Distribution. Moist tropical forests, along streams, and moist disturbed sites below 500 m

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elevations in Belize, Guatemala, and the states of Campeche, Chiapas, Oaxaca, Tabasco, and Veracruz, Mexico (Fig. 2).

Acacia usumacintensis is a tall tree that is a common component of lowland tropical rainforests in Guatemala and southern Mexico. No specimens of this species have been observed by the present authors farther south than Guatemala and Belize. Specimens labeled A. usumacintensis from Nicaragua are the result of confusing this taxon with various species of Lysiloma. Acacia usumacintensis specimens are commonly misidentified as L. acapulcensis (Kunth) Benth. Thompson (1980), in a revision of Lysiloma, annotated the type of A. usumacintensis as L. acapulcensis. This specimen (E. Matuda 3550), however, is A. usumacintensis, having numerous separate filaments remaining at the base of some of the fruits.

brown to greenish brown, not flexuous, glabrous; short shoots absent. Leaves alternate, 40-120 mm long, stipules herbaceous, light brown, narrowly triangular, to 1.3×0.3 mm near the base, glabrous, persistent; petiole adaxially shallowly grooved, 30-80 mm long, glabrous; petiolar gland solitary, located on the lower half of the petiole, sessile, circular to more commonly elliptic, 1.0-2.5 mm long, flattened or with slightly raised margins, glabrous (Fig. 4C); rachis adaxially grooved, 20-62 mm long, lightly puberulent, a sessile, saucer-shaped gland, 0.6-1.5 mm across, between the pinnae of the upper 1 to 2 pinna pairs; pinnae 2 to 6(8) pairs per leaf, 40–75(90) mm long, 4–9 mm between pinna pairs; petiolules 2.5-4.0 mm long; leaflets 36 to 65 pairs per pinna, opposite, 0.7-1.1 mm between leaflets, oblong, $3.5-5.5(7.5) \times 0.8-1.3$ mm, glabrous, lateral veins usually not obvious, only one vein from base, base oblique, margins ciliate, apex acute to obtuse. Inflorescence a loosely flowered cylindrical spike 20-90 mm long, 1 to 3 from the leaf axil, or rarely in terminal racemose clusters; peduncle 3–10 \times 0.5–0.9 mm, glabrous to lightly puberulent; involucre absent; floral bracts linear, to 1 mm long, glabrous to lightly pubescent, usually not deciduous. Flowers sessile, creamy-white; calyx 5lobed, 0.5–1.0 mm long, lightly appressed pubescent; corolla 5-lobed, 1.2-2.2 mm long, lightly appressed pubescent; stamen filaments 3-5 mm long; ovary glabrous, on a stipe to 0.3 mm long. Legumes light yellowish green to light brown, straight, flattened, oblong, $80-130 \times 13-20$ mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 12 mm long, apex acute to acuminate. Seeds not seen. Flowers: April-July.

Representative specimens. (*used in PCA analysis) BELIZE. El Cayo Dist., Benque Viejo, Río Mopán, Contreras 7089 (CAS, F, LL, MO*, NY); vicinity Georgeville, Western hwy., Dwyer 12662 (MO, US*); Valentin, El Cayo, Lundell 6356 (F, GH, MICH*). GUATEMALA. Izabal: Puerto Barrios, ca. 20 km from town on the road to Machacas, Marshall, Castillo & Marshall 423 (MO, NY*). Petén: Lacandón, about 2 km S, Contreras 3467 (CAS, F, LL*, MO); Macanche, Contreras 5479 (F, MICH*, US); Dos Lagunas, 19 Apr. 1969, Contreras 8356 (F*, LL, MO); Tikal, in ramonal on Main Plaza, Lundell 15348 (CAS*, F, LL, MO, NY); Tikal, around Aguada Tikal, Lundell 15973 (F*, LL, NY); Sayaxche, in corozal about 5 km S of village, Lundell 18071 (F, LL, MO, NY*); Cadenas, on river bank bordering Río Gracios, Lundell & Contreras 19033 (F*, LL, NY). MEXICO. Campeche: El tormento Escárcega, Sousa, Cabrera, Davidse & Chater 12369 (ILL, MO*). Chiapas: W side of Laguna Miramar E of San Quintín, Breedlove 33387 (DS*, MICH, MO); 20 km al SE de la desviación San Javier Frontera Echeverría hacia Río Lacantum, Chimal, Durán & Quintanilla 755 (F, ILL, MO*); a 5 km al E de Crucero Corozal, camino a Frontera Corozal, Ocosingo, Martínez 7291 (MO, NY*); a 15 km al E de Nvo. San Juan Chamula camino a Ixcan, Martínez & Girón 6288 (MO*, MU). Oaxaca: Rincón Bamba, al O de Salina Cruz, Martínez 629 (MO*). Tabasco: Mun. Balancán, por la carretera O, por el Poblado Arroyo del Triunfo, Calzada 2385 (F*, NY); La Palma, Balancán, Matuda 3324 (F, MICH*, WIS). Veracruz: Mpio. Minatitlán, Lo-

Distribution. Common in thorn-scrub thickets, and disturbed dry forests in the lowlands of the states of Campeche, Quintana Roo, and Yucatán (Fig. 2).

Restricted to the Yucatán Peninsula, Acacia dolichostachya appears to be a relatively common component of thorn-scrub thickets and disturbed sites. The fact that most leaves have fewer than seven pinna pairs separates A. dolichostachya from most other species of this group. Other species with six or fewer pinna pairs differ by having pinnae with fewer than 35 pairs of leaflets, along with smaller leaflets (A. compacta), much longer petioles (A. willardiana), or pubescent leaves (A. mammifera and A. sericea).

mas al SW de La Garganta, 5.8 km al W de Uxpanapa, Wendt, Villalobos & Navarrete 4127 (F, MICH, MO, TEX).

 Acacia dolichostachya S. F. Blake, Proc. Biol. Soc. Washington 34: 43. 1921. Senegalia dolichostachya (S. F. Blake) Britton & Rose, N. Amer. Fl. 23: 112. 1928. TYPE: Mexico. Yucatán: Las Bocas de Silam, May 1916, G. J. Gaumer & Sons 23329 (holotype, F!; isotypes, F!, G!, K!, NY photo!).

Small tree to 15 m tall with bark dark brown to dark gray, scaly in rectangular plates; twigs light

Considering the restricted distribution of this species, the only other taxon that *A. dolichostachya* might be confused with is *A. usumacintensis*. Both taxa have more than 35 pairs of leaflets on each

pinna, flattened petiolar glands on the lower half of the petiole, and petiolules that are more than 2.5 mm long. They are easily separated as *A. dolichostachya* has fewer pinna pairs per leaf (mostly six or fewer), smaller stipules (less than 1.3 mm long), less distance between the leaflets on the pinna rachis (less than 1.2 mm), and smaller sepals (mostly less than 1.0 mm long).

Representative specimens. MEXICO. Campeche: 4

berulent; short shoots absent. Leaves alternate, 50-150 mm long; stipules herbaceous, light brown, narrowly linear, to 3×0.5 mm near the base, usually glabrous, persistent; petiole adaxially shallowly grooved, 15-40 mm long, \pm glabrous, but commonly with minute purple glands; petiolar gland solitary, located between the lower pinna pairs or along the upper half of the petiole, sessile, nearly circular to slightly elongated, 0.7-2.3 mm long, saucer- to cup-shaped, glabrous, rarely absent; rachis adaxially grooved, 20-110 mm long, glabrous to lightly puberulent and usually with minute purple glands, a sessile, cup-shaped gland, 0.4-0.9 mm across, between the upper pinna pair; pinnae 7 to 30 pairs per leaf, 25-60 mm long, 3-7 mm between pinna pairs; petiolules 1.0-2.4 mm long; leaflets 36 to 60 pairs per pinna, opposite, 0.5-1.2 mm between leaflets, linear, $2.5-4.8 \times 0.7-1.1$ mm, glabrous and commonly light greenish purple above, lateral veins obvious, a midvein and 1 to 2 smaller veins from the base, base oblique, margins ciliate, apex narrowly acute to acuminate. Inflorescence a loosely flowered cylindrical spike 40-100 mm long, 1 to 4 from the leaf axil; peduncle 5-10 \times 0.5–1.0 mm, glabrous to lightly puberulent and commonly with scattered minute purple glands; involucre absent; floral bracts linear, to 1 mm long, early deciduous. Flowers sessile, creamy-white; calyx 5-lobed, 1.0–1.6 mm long, lightly appressed pubescent; corolla 5-lobed, 2.1-2.8 mm long, lightly appressed pubescent; stamen filaments 4.5-6.5 mm long; ovary glabrous, on a stipe to 0.4 mm long. Legumes light to dark brown, straight, flattened, oblong, 80–170 \times 13–25 mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 20 mm long; apex broadly acute. Seeds uniseriate, no pulp, dark reddish brown, oval, strongly flattened, $7-10 \times 4.5-7.2$ mm, smooth; pleurogram U-shaped, 1.2–2.3 mm across. Flowers: March-June.

km despues de Sho laguna Xmaben, Mpio. Hopelchen, Chan & Ucan 1023 (UC*); a 12 km al E de Constitución, o sea a 15 km al W de Conhuas, Sousa, Ramamoorthy, Ibarra, Rico & Basurto 12229 (MO*). Quintana Roo: En Rancho San Felipe, a 7 km al S de la desviación a Puerto Morelos, por la carretera Cancún-Tulum, Cabrera 11456 (MO*); a 15 km al N de la desviación a Puerto Morelos, sobre la carretera Tulum-Cancún, Cabrera & Cabrera 3158 (MO*); a 12 km al E de Carrillo Puerto, rumbo a Vigia Chico, Cabrera & Cabrera 3561 (MO*); a 35 km al NW de Carrillo Puerto, sobre el camino a Vigia Chico, Cabrera & Cabrera 4080 (MO*); en el km 2 del camino al Faro de la Punta Celarain, Isla de Cosumel, Cabrera & Cabrera 10555 (MO*); Jardín Botánico Quintana Roo, Duran, Olmsted & Honorato 85 (MO*); 3-4 mi. S of Filipe Carrillo Puerto, Dwyer, Spellman, Vaughan & Wunderlin 258 (MO*); 5 km al N de Puerto Morelos, Grether, Quero & Flores 1331 (MO*); a 6 km al N de Puerto de Morelos a Cancún, Sousa, Téllez & Cabrera 10959 (MO*); a 48 km al NE de Filipe Carrillo Puerto, Sousa, Cabrera, Davidse & Chater 12441 (MO*); al NW del entronque Chetumal-F. Carrillo Puerto, sobre carretera Mérida via Corta, Téllez & Cabrera 2012 (MO*); a 10 km al S de Tulum, Téllez & Cabrera 2032 (MO, NY*); a 15 km al N de Bacalar, Téllez & Cabrera 2366 (NY*); 10 km antes de la entrada a Buenavista, de Chetumal rumbo a Felipe Carrillo Puerto, Ucan & Flores 985 (UC*). Yucatán: 11.2 km N of Dzibilchaltum turn on road from Mérida to Progreso, Bradburn & Darwin 1294 (MO, NY*); 4.6 km al E de Sucila, sobre la carretera Tizimin-Mérida, Cabrera & Cabrera 13203 (MO*); near Piste, Lundell & Lundell 7344 (A, F, LL, MICH*, MO, US); 7 km al S de Yaxcaba, Vara, Arias & Isely 574 (CAS, F*, MO).

3. Acacia acatlensis Bentham, London J. Bot. 1: 513. 1842. Senegalia acatlensis (Bentham) Britton & Rose, N. Amer. Fl. 23: 112. 1928. TYPE: Mexico. Puebla: Acatlán, May 1830, G. Andrieux 396 (holotype, K!, F photo!, MICH)

Distribution. Dry, deciduous, tropical forests and thorn-scrub forests between 500 and 2100 m elevations in the states of Chiapas, Guerrero, Jalisco, México, Michoacán, Oaxaca, and Puebla, Mexico (Fig. 2).

photo!, NY photo!, TEX photo!; isotypes, G!, US!).

Senegalia submontana Britton & Rose, N. Amer. Fl. 23: 113. 1928. TYPE: Mexico. Oaxaca: Cerro San Antonio, alt. 1800 m, 12 Oct. 1907, C. Conzatti 2046 (holotype, US!; isotypes, F!, MEXU!, NY!). [Britton and Rose (1928) listed the type as Conzatti 25,346. On the NY isotype, Britton wrote "the number of this specimen was erroneously printed 25,346."]

Shrub or small tree to 15 m tall with bark dark gray, shallowly furrowed; twigs light brown to greenish brown, not flexuous, glabrous to lightly puAcacia acatlensis is very similar morphologically to A. centralis. Both are widely distributed in southern Mexico, although A. centralis has been collected more frequently in the very south of Mexico and, unlike A. acatlensis, it occurs across the border in Guatemala and countries to the south (see Fig. 2). These two species are difficult to separate, and it is possible that they should be considered as subspecies of a single species. The two can be sepa-

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rated based on the presence or absence of minute purple glands that are common at the base of the leaflets, in the grooves of the rachis and petiole, and not uncommon along the axis of the inflorescence in A. acatlensis. Rarely these glands are clear, lacking the purple color, but are easily observed under magnification. None of these minute glands were found on specimens of A. centralis examined. No other characteristics could be found that consistently separate these two species, though most specimens of A. centralis have leaflets with long hairs at the base on the ventral surface. These hairs are particularly evident on young leaflets, sometimes falling off as the leaves mature. Acacia acatlensis is also similar to A. usumacintensis, differing by having narrower leaflets (less than 1.1 mm across) and lacking the large flattened petiolar gland of that taxon. Acacia acatlensis is sympatric with A. sericea and A. mammifera in Oaxaca; these two taxa also have minute purple glands on the leaves. Acacia acatlensis is easily separated from A. mammifera, which has fewer than 33 pairs of leaflets per pinna, leaflets that are commonly more than 1.5 mm wide, and a stalked petiolar gland. The dense, erect pubescence of A. sericea petioles and fruits usually separates this species from A. acatlensis.

negalia centralis Britton & Rose, N. Amer. Fl. 23: 113. 1928. TYPE: El Salvador. Near San Salvador, 1923, S. Calderón 1774 (holotype, NY!; isotypes, BM!, F!).

Tree to 25 m tall with bark dark grayish brown, vertically fissured, rough and scaling; twigs light brown to greenish brown, not flexuous, mostly glabrous; short shoots absent. Leaves alternate, 70– 180 mm long; stipules herbaceous, light brown,

narrowly linear, to 4.5×0.6 mm near the base, glabrous, persistent; petiole adaxially shallowly grooved, 18-46 mm long, glabrous to lightly puberulent; petiolar gland solitary, located on the middle part of the petiole, sessile, usually circular, 1.0-2.6 mm across, saucer- to cup-shaped, glabrous; rachis adaxially grooved, 40-150 mm long, glabrous to puberulent, a sessile, saucer- to doughnut-shaped gland, 0.6-1.3 mm across, between the pinnae of the upper 1 to 2 pinna pairs (Fig. 4F); pinnae (7)11 to 24 pairs per leaf, 30-70 mm long, 3-9 mm between pinna pairs; petiolules 0.8-1.5 mm long; leaflets 40 to 60 pairs per pinna, opposite, 0.5-1.2 mm distance between leaflets, linear, $3.0-5.5 \times 0.6-1.1$ mm, glabrous except for usually some long hairs at the base beneath, lateral veins obvious, with a midvein and 1 to 2 smaller veins from the base, base oblique, margins ciliate, apex narrowly acute to acuminate. Inflorescence a loosely flowered cylindrical spike 60-140 mm long, 1 to 3 from the leaf axis, or in terminal racemose clusters; peduncle 4–10 \times 0.5–1.0 mm, glabrous to lightly puberulent; involucre absent; floral bracts linear, to 1 mm long, pubescent, early deciduous. Flowers sessile, creamy-white; calyx 5-lobed, 0.7-1.3 mm long, lightly appressed pubescent; corolla 5-lobed, 1.8-2.5 mm long, lightly appressed pubescent; stamen filaments 4.5-6.5 mm long; ovary glabrous, on a stipe to 0.3 mm long. Legumes light brown, straight, flattened, oblong, 100–160 \times 16– 28 mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 20 mm long; apex broadly acute to obtuse and usually apiculate. Seeds uniseriate, no pulp, dark reddish brown, nearly circular, strongly flattened, 6-9 mm across, smooth; pleurogram U-shaped, 1.5-3.0 mm across. Flowers: April-August, and sporadically throughout the year when moisture is available.

Representative specimens. MEXICO. Chiapas: a 4 km al SW de Toliman, Sousa, Ramamoorthy, Cortés & Hernández 11824 (MO*, TEX). Guerrero: Tario, Coyuca Dist, Hinton 7755 (DS, GH, MICH, NY, US); en el Puerto El Salado, a 7 km al N de Tlapa camino a Huamuxtitlán, Martínez 1070 (MO, TEX*). Jalisco: 2 km al W de El Mirador, 10 km al NE de El Corcobado, carretera Autlán-Guadalajara, Magallanes 2169 (MO*); a 20 km al NW de San Patricio, Magallanes 2420 (MO*); 20 km NE of Autlán, McVaugh 23271 (MICH*, MO, NY); Barranca de Los Tanques, desviación al camino San Martín de las Cañas, Villarreal 6121 (MICH*). México: Pungarancho, Temascaltepec Dist., Hinton 3747 (F, GH*, MO, NY, US). Michoacán: 3 km al S de Jungapeo, Soto, Aureolea, Silva & Pizarras 8573 (MEXU*). Oaxaca: 5 km sobre la desviación a Barranca de Los Calabazos, Aguilar 220 (NY*); 3 km al NE de Tonala, carretera a Huajuapán, Calzada & Campos 18320 (CAS*, MICH, MSC); cave area near Mitla, near pass to Díaz Ordaz, Kirkby 10 (US*); 2.5 km al N de Yosocuta en la carretera Huajuapán-Juxtlahuaca, Magallanes, Ramos & Magallanes 11 (CAS*, LL, MO); 3 km al NW de Santo Domingo Tonala, carretera a Huajuapán, Ortíz-Bermudez 291 (MEXU*); Tomellín Canyon, Pringle 5885 (GH, MICH, US*, VT); cerca de Tonala, Rzedowski 34920 (CAS*, MO); Subida a las Ruinas del Cerro Guiengola, Torres, Torres, Cortéz & Martínez, 928 (MO*); Ladera Oriente del Cerro Guiengola, Torres, Torres, Téllez & Martínez 400 (MO*). Puebla: Tepeji de Rodríguez, Felger 85-38 (MO*); 29 mi. SE of Acatlán on hwy. 190, Seigler & Maslin 12692 (EIU*, ILL).

4. Acacia centralis (Britton & Rose) Lundell, Contr. Univ. Michigan Herb. 4: 7. 1940. SeDistribution. Lowland forests, and moist disturbed sites below 1300 m in Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and the states of Chiapas, Jalisco, Oaxaca, and Sinaloa, Mexico (Fig. 2).

A tall tree, sometimes entering the canopy of moist lowland forests, *Acacia centralis* is also a

common component of disturbed habitats at lower elevation through most of Central America. Most collections are from roadsides, disturbed pastures, and gallery forests. In addition to its close morphological similarity to Acacia acatlensis discussed above, A. centralis is also sympatric with five other acacia species in southern Mexico. Of these, it is easily separated from A. compacta and A. mammifera, as these species have fewer pinna pairs per leaf (fewer than 7) and fewer leaflets per pinna (fewer than 36). The erect hairs of A. sericea, the larger leaflets of A. usumacintensis, and the exfoliating bark of A. salazari can be used to distinguish these species from A. centralis. The authors have frequently encountered specimens of A. centralis that were annotated Albizia niopoides (Benth.) Burkart. Flowering material of these two taxa is easily separated by the filament-tube and fewer stamens in Albizia. Fruiting material and sterile specimens also can be separated, as in A. centralis, the leaflets are less than 5.5 mm long and have an acuminate apex, whereas in Albizia niopoides, the leaflets are longer, mostly more than 5.5 mm long, and the apex is broadly acute to obtuse.

June 1899, J. N. Rose & W. Hough 4680 (holotype, US!; isotypes, GH!, K!, NY!).

Lysiloma standleyana Britton & Rose, N. Amer. Fl. 23: 81. 1928. TYPE: Mexico. Oaxaca: Tomellin, Sept. 1905, J. N. Rose 10082 (holotype, NY *!, F photo!, MO photo!).

Shrub or small tree to 3(4) m tall with bark dark gray, flaking off in thin strips; twigs light brown to dark reddish brown, slightly flexuous, pubescent to glabrous, when young with minute purple glands; short shoots commonly present above the nodes, to 3 mm long, covered with acuminate stipules and old leaf bases. Leaves alternate, also commonly clustered on the short shoots, 5-30 mm long; stipules herbaceous, light brown, narrowly linear, to 3 \times 0.4 mm near the base, usually glabrous, persistent; petiole adaxially grooved, 2.5-14.0 mm long, usually pubescent and with minute purple glands; petiolar gland solitary, located at or just below the lower pinna pair, sessile, circular, 0.4-1.1 mm across, doughnut-shaped, glabrous (Fig. 4H); rachis adaxially grooved, 0-20 mm long, usually pubescent and with minute purple glands, a sessile, saucer-shaped gland, 0.2-0.6 mm across, occasionally present between the upper pinna pair; pinnae 1 to 6 pairs per leaf, 6-18 mm long, 2-5 mm between pinna pairs; petiolules 0.5-1.1 mm long; leaflets 9 to 22 pairs per pinna, opposite, 0.5-0.9 mm distance between leaflets, oblong, 1.4–3.0 \times 0.5–0.9 mm, glabrous above, usually lightly pubescent beneath with long hairs, lateral veins not obvious, only one vein from the base, base oblique, margins usually ciliate, apex acute to obtuse. Inflorescence a loosely flowered cylindrical spike 30-70 mm long, solitary (rarely 2 to 3) from the leaf axil; peduncle 6–13 \times 0.4–0.7 mm, usually pubescent and with minute purple glands; involucre absent; floral bracts linear, to 1.5 mm long, pubescent, early deciduous. Flowers sessile, creamy-white; calyx 5lobed, 1.1–1.7 mm long, densely appressed pubescent; corolla 5-lobed, 2-3 mm long, densely appressed pubescent; stamen filaments 5.5–7.5 mm long; ovary glabrous, on a stipe to 0.4 mm long. Legumes light yellowish brown, straight, flattened, oblong, 50–120 \times 10–16 mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 8 mm long; apex acuminate and usually beaked. Seeds uniseriate, no pulp, purplish brown, near circular, strongly flattened, 5-8 mm across, smooth; pleurogram U-shaped, 1.3–2.2 mm across. Flowers: April–July.

Representative specimens. COSTA RICA. Guana-

caste: vicinity of Cañas, Daubenmire 775 (F*); Santa Rosa National Park, Janzen 10355 (MO*). Puntarenas: San Luis village, Haber & Bello 1628 (MO*). EL SAL-VADOR. vicinity of Comasagua, Allen & Armour 7257 (F, LL, NY, US*). GUATEMALA. Petén: Laguna Yaxja, Harmon & Dwyer 2763 (F*, LL). Zacapa: Gualán, Deam 6281 (A, F, GH*, MO, NY, UC, US, VT). HONDURAS. Morazán: Alrededores de la Ciudad Universitaria, Torres 183 (NY*). Paraiso: 15 kms S of El Paraiso, Molina 18420 (NY, US*). MEXICO. Chiapas: Siltepec, Matuda 1584 (A, MICH*, NY, US). Jalisco: 5 km al SE de La Manzanilla, carretera Puerto Vallarta-Barra de Navidad, Magallanes 906 (F, MEXU). Oaxaca: Pto. San Bartolo, Yautepec, MacDougall H230 (MICH, NY*); between Limón and Zapote, MacDougall s.n. (NY*, US). Sinaloa: Mauto, Los Tepemesquites, Ortega 5717 (GH, US). NIC-ARAGUA. L(on: Volcán Momotombo, near Punta El Diablo, Neill 480 (MO, NY). Managua: Las Nubes, El Crucero, García 96 (MO*); vicinity of Managua, Garnier 957 (F, MICH*, US); Managua, Punta Chiltepec, Grijalva, Vanegas & Sánchez 3105 (CM, MO*); Esquipulas, Hall & Bockus 7981 (MO, NY*, UC); Peninsula de Chiltepec, Punta Chiltepe, Moreno 16917 (CM, MO*); along hwy. 8, km 28, Stevens 3922 (MO*); 1.9 km from hwy. 2 on road along ridge of Sierra de Managua, Stevens 4753 (MO*); 1 km SW of Laguna Apoyeque, Vincelli 779 (MO*). Masaya: Laguna de Apoyo, Moreno 21308 (MO). Rivas: Quebrada Las Cañas, near Río Escalante, Stevens 9681 (MO).

 Acacia compacta Rose, Contr. U.S. Natl. Herb. 8: 31. 1903. Senegalia compacta (Rose) Britton & Rose, N. Amer. Fl. 23: 111. 1928. TYPE: Mexico. Oaxaca: Tomellin Canyon, 24

Distribution. Thorn-scrub forests, thickets, rocky slopes and washes between 500 and 1600 m

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elevation in the states of Puebla and Oaxaca (Fig. 3).

Acacia compacta, a much-branched shrub that rarely exceeds 3 m, has a very restricted distribution, occurring in southeastern Puebla and adjacent Oaxaca. Even there it does not appear to be a common species, relatively little material being available for study. All material examined is from xeric habitats, usually on rocky slopes and in washes, where A. compacta forms small thickets (Rico Arce & Rodríguez, 1998). The short shoots at many of the nodes, small leaflets (mostly less than 2.5 mm long), leaves that are less than 30 mm (mostly less than 20 mm) long, and fruits with the apex acuminate and beaked, separate A. compacta from other members of this group. The presence of short shoots is probably an adaptation to xeric conditions. Acacia compacta shows variation with regard to several important characteristics. Leaf size is highly variable: the leaves that develop on the short shoots are usually smaller and have shorter petioles and fewer pinna pairs; whereas the leaves that form on fast-growing shoots are larger, the petioles sometimes reach a length of 14 mm, and 5 or 6 pinna pairs develop along the rachis. The shape and structure of the petiolar gland is also somewhat variable. The majority of the specimens have a sessile petiolar gland that is doughnut- or torus-shaped, although a few specimens have a stalked petiolar gland with a bulbous apex. Generally, these glands are found on young leaves forming on the short shoots; other leaves have sessile, doughnut-shaped glands. It is possible that Acacia compacta may rarely hybridize with A. mammifera, the only other species of this group with stalked petiolar glands.

km al SE de San Rafael, Sousa, Sousa & Basurto 10430 (CAS*, TEX); Cerro Tepetroja al SW de Axusco, Tenorio & Romero 9043 (CAS*); Jardín Botánico de Cactáceas y Suculentas de Zapotitlán de las Salinas, Valiente-Banuet & Maeda 674 (RSA, TEX*); Jardín Botánico de Cactáceas y Suculentas de Zapotitlán de las Salinas, Valiente-Banuet & Maeda 706 (RSA*).

6. Acacia sericea Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(2): 311. 1843. Senegalia sericea (Martens & Galeotti) Britton & Rose, N. Amer. Fl. 23: 111. 1928. TYPE: Mexico. Puebla: Tehuacán, alt. 6000 ft., May 1840, H. Galeotti 3345 (holotype, BR!; isotypes, K!, P!, MICH photo!, NY photo!).

Acacia pueblensis Brandegee, Univ. California Publ. Bot.
4: 85. 1910. TYPE: Mexico. Puebla: Cerro de Solunte, alt. 7000–8000 ft., June 1909, C. A. Purpus 3863 (holotype, UC!, MEXU photo!; isotypes, BM!, MO!, NY!, US!).

Shrub or small tree 3 to 4(6) m tall with bark dark gray, cracked and fissured, breaking away and leaving dark purplish brown, smooth areas; twigs dark brown to purplish brown, not flexuous, glabrous to lightly pubescent; short shoots absent. Leaves alternate, 30–120 mm long; stipules herbaceous, light brown, narrowly linear, to 4×0.4

Representative specimens. MEXICO. Oaxaca: 52 km al S de Tecomavaca por la carretera rumbo a la Ciudad de Oaxaca, Salinas & Dorado F-2670 (MEXU, TEX*); 3 km al W de San Gabriel, Salinas & Ramos F-3857 (ARIZ*, F, MEXU, RSA); 14 km al N de Cuicatlán, Sousa, Martínez, Téllez & Magallanes 5394 (CAS*, US, WIS); a 3 km al NW de Guadalupe Los Obos, o sea a 10 km al NW de Cuicatlán, Sousa, Téllez, Magallanes & Delgado 6912 (MICH*). Puebla: Alrededores del lado W del pueblo de Axusco, Chiang, Salinas & Dorado F-2466 (ARIZ, MO, RSA*); en la desviación a San Luis Atolotitlán y Los Reyes Metzontla, Medrano, Chiang, Davila & Villaseñor 1905 (ARIZ*, MO*); 18 km al NW de Teotitlán del Camino, a Tehuacán, Medrano, Jaramillo, Villaseñor, Ruiz & Singer F-1172 (MO*); vicinity of San Luis Tultitlanapa, Purpus 3193 (F, GH*, MO, NY, UC, US); 3 km al SE de San Rafael, Rico, Ramos & Hernández 246 (CAS*, MO); Cerro de La Escalera, Ejido de San José Tilapa, Rico, Ramos & Hernández 248 (CAS*, MO); 1 km al NE-E del limite estatal Oaxaca-Puebla por la carretera Huajuapan de León-Tehuacán, Salinas & Dorado F-3199 (F*); a 2 km al SE de San Rafael, cerca de los limites Puebla-Oaxaca, Sousa & Sousa 10405 (ARIZ*, TEX); a 2 mm near the base, glabrous to pubescent, sometimes tardily deciduous; petiole adaxially grooved, 10-30 mm long, densely pubescent with erect hairs and scattered minute purple glands; petiolar gland solitary, located along the upper half of the petiole, sessile, circular to elliptic, 0.6-1.2 mm long, saucer-shaped to cup-shaped, glabrous, sometimes absent; rachis adaxially grooved, 15-100 mm long, pubescent with erect hairs and scattered minute purple glands, a sessile, saucer-shaped gland, 0.5-1.1 mm across, between the pinnae of the upper 1 or 2 pinna pairs; pinnae 5 to 13 pairs per leaf, 25-49 mm long, 4-8 mm between pinna pairs; petiolules 1.5-2.1 mm long; leaflets 14 to 35(44) pairs per pinna, opposite, 0.7-1.3 mm interval between leaflets, linear, $2.5-5.0 \times 0.8-1.5$ mm, pubescent on both surfaces with appressed to erect hairs, lateral veins obvious with only one vein from the base, base oblique, margins ciliate, apex acute to obtuse. Inflorescence a densely flowered cylindrical spike 30-80 mm long, solitary from the leaf axil; peduncle 3-20 \times 0.7-1.2 mm, densely pubescent with erect hairs; involucre absent; floral bracts linear, to 3.5 mm long, densely pubescent, deciduous. Flowers sessile, creamy white; calyx 5-lobed, 1.5-2.2 mm long, densely pubescent with erect hairs; corolla 5-lobed, 2.0-3.0 mm long, densely pubescent with erect hairs; stamen filaments 6-8 mm long; ovary glabrous, on a stipe to 0.3 mm long. Legumes

light yellowish brown, straight, flattened, oblong, 90–170 \times 15–24 mm, cartillaginous, transversely striate, pubescent, eglandular but usually with minute purple glands when young, dehiscent; stipe to 14 mm long; apex acuminate and apiculate to 5 mm long. Seeds uniseriate, no pulp, dark purplish brown, nearly circular, strongly flattened, 5.0-8.5 mm across, smooth; pleurogram U-shaped, 1.5-2.5 mm across. Flowers: February-June.

F-2024 (MO, NY*); Tehuacán, Conzatti 2176 (F*, US); 3 mi. N of the city limits of Tehuacán, Hansen, Hansen & Nee 1728 (LL, MICH, US*, WIS); about 10 mi. N of Tehuacán on main road toward Orizaba, Hughes, Lewis & Contreras 1320 (MEXU, NY*); Cerro de Solumta, Purpus 3863 (MO*); Tehuacán, Purpus 5845 (F, MO, NY*, UC, US); Tehuacán, Purpus 10682 (NY, US*); Acatepec, SW Zapotitlán, Sousa 2668 (CAS*, US); Ladera W de Cerro Grande Mpio. Caltepec, Tenorio & Romero 5424 (CAS*); Barranca de Los Membrillos, al SW de Caltepec, Tenorio, Torres & Romero 3784 (CAS*).

Distribution. Rocky desert and dry thorn-scrub forests from 1100 to 2000 m elevation in Puebla and Oaxaca, Mexico (Fig. 2).

A small tree, mostly 3 or 4 m tall, Acacia sericea is known from southeastern Puebla and adjacent Oaxaca. It occurs at higher elevation, usually above 1100 m elevation, in desert and thorn-scrub forests. Most collections are from roadsides, usually in dry, disturbed habitats, and many are from the Tehuacán valley (Rico Arce & Rodríguez, 1998). Based on the number of specimens available for study, this taxon is not a common component of the vegetation.

Acacia sericea is distinct from most other members of this group. The dense, erect pubescence on most parts of the plant makes it easy to distinguish this taxon. The leaf rachis, the pinna rachis, and usually the petiole are densely pubescent with erect hairs that exceed 0.3 mm in length. The leaflets are mostly pubescent with erect to slightly appressed pubescence, whereas the mature fruits are short pubescent. Also, the calyx and corolla are pubescent with erect hairs, as are the floral bracts, which are commonly longer than those found in other members of this group. Acacia sericea possibly hybridizes with A. acatlensis in areas where they are sympatric. Occasional specimens were encountered with reduced pubescence and many leaflet pairs per pinna, characteristics usually associated with A. acatlensis.

7. Acacia mammifera Schlechtendal, Linnaea 12: 563. 1838. Senegalia mammifera (Schlechtendal) Britton & Rose, N. Amer. Fl. 23: 112. 1928. TYPE: Mexico. Hidalgo: Barranca de Acholoya, C. Ehrenberg s.n. (holotype, HAL!; isotype, UC!).

Shrub or small tree to 5 m tall with bark dark gray, shallowly fissured; twigs light brown to purplish brown, not flexuous, usually puberulent and, when young, commonly with minute purple glands; short shoots absent. Leaves alternate, 30-130 mm long; stipules herbaceous, light brown, narrowly triangular, 2.5×0.6 mm near the base, glabrous to puberulent, persistent; petiole adaxially grooved, 8-50(70) mm long, usually lightly puberulent and commonly with minute purple glands; petiolar gland solitary, located between the lower pinna pair or rarely along the upper half of the petiole, stalked, circular, 0.4-0.8 mm across, apex globose, glabrous (Fig. 4D); rachis adaxially grooved, 10-70 mm long, puberulent and commonly with minute purple glands, with a stalked gland with a globose apex, 0.4-0.6 mm across, between most pinna pairs; pinnae 1 to 6(9) pairs per leaf, 30-85 mm long, 6-15(25) mm between pinna pairs; petiolules 2.0-2.8(4.5) mm long; leaflets 10 to 26(33) pairs per pinna, opposite, 1-5 mm between leaflets, oblong, 4–12 \times 1.5–3.5(4.5) mm, loosely pubescent on both surfaces with appressed hairs, commonly purplish above, light green to purplish green beneath, lateral veins obvious with a midvein and 1 to 3 smaller veins from the base, base oblique, margins ciliate, apex obtuse to broadly acute. Inflorescence a loosely flowered cylindrical spike 30-90 mm long, solitary (rarely 2) from the leaf axil; peduncle 6-15 \times 0.7-1.1 mm, puberulent and with minute purple glands; involucre absent; floral bracts linear, to 1.4 mm long, pubescent, early deciduous. Flowers sessile, creamy-white; calyx 5lobed, 1.3-2.0 mm long, lightly appressed pubescent; corolla 5-lobed, 2.2-3.5 mm long, lightly appressed pubescent; stamen filaments 6.5-8.5 mm long; ovary glabrous, on a stipe to 0.3 mm long. Legumes light yellowish brown to dark greenish

Representative specimens. MEXICO. Oaxaca: Cuesta inferior de Salome, Districto de Cuicatlán, Conzatti 5321 (NY*); Cuesta de ruta Vieja, Smith 430 (GH*); a 8 km al NE de Teotitlán del Camino, carretera a Huautla, Sousa 6923 (CAS, MEXU, MO, UC*); a 12 km al N de Tonaltepec, Sousa & Magallanes 8917 (ISC*); a 8 km al NE de Teotitlán del Camino, en el camino a Huautla, Sousa, Martínez, Téllez & Magallanes 5396 (CAS, MEXU*, US, WIS); a 9 km al NE de Teotitlán del Camino, Sousa, Martínez, Téllez & Magallanes 5402 (CAS*, US); a 9 km al N de la desviación a Tonaltepec, Sousa, Ramos & Téllez 6131 (CAS, MO, SD*, WIS); a 8 km al E-NE de Teotitlán del Camino, camino a Huautla, Sousa, Téllez, Germán & Rico 8083 (CAS*); Cañada de Carrizalillo, Cerro Verde, Tenorio, Romero, Martínez & Tenorio 6983 (F, MEXU*); 7.6 km al E de Teotitlán, carretera a Huautla de Jiménez, Torres & Martínez 6499 (MEXU*, MO). Puebla: Cerros calizos al NE de Tehuacán, Chiang, Villaseñor & Durán

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brown, straight, flattened, oblong, $80-240 \times 18-35$ mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 12 mm long; apex acuminate and usually beaked. Seeds uniseriate, no pulp, dark brown, nearly circular, strongly flattened, 8.0-10.5 mm across, smooth; pleurogram U-shaped, 3-4 mm across. Flowers: April-June.

Distribution. Thorn-scrub forests and from the pinyon-juniper zone in dry thickets, and rocky slopes from 1300 to 2700 m elevation in eastern Mexico from the states of Tamaulipas and Nuevo León south to Oaxaca (Fig. 3). Acacia mammifera is widely distributed throughout the central part of Mexico from the state of Oaxaca, north to Tamaulipas and Nuevo León. It does not appear to be a common species, however, many of the collections being from near the same localities in the various states. All collections examined are from above 1300 m, many from near the pinyon-juniper zone, or from rocky slopes and dry thickets, mostly associated with thorn-scrub vegetation. The few pinna pairs, the large leaflets with appressed hairs on both surfaces, the dull purple color on the upper surface of the leaflets, the narrowly triangular stipules, and the stalked petiolar glands can be used to separate Acacia mam*mifera* from other members of this group. This wide-ranging species is not extremely variable morphologically, but one unusual specimen from Puebla, Mexico, was encountered [E. M. Martínez S. 21665 (MEXU)]. This was a small, compact plant with the small leaves and leaflets of A. compacta, but was similar to A. mammifera in lacking short shoots, having narrowly triangular stipules, a stalked petiolar gland with a bulbous apex, and leaflets that were purplish and pubescent on both surfaces. Occurring at an elevation of 2300 m, this specimen was probably outside the natural range of A. compacta. The status of this possible hybrid must await additional field studies.

Romero 5777 (ARIZ*, CAS, CM, TEX, WIS); Cerro Tepearco, al E de el Rancho de Tlacuiloltepec, Tenorio & Romero 8814 (MO*, RSA, TEX). Querétaro: about 80 km NE of Querétarc on road to Pinal de Amoles, McVaugh 10364 (GH, LL, MICH*, MO, TEX, US); 3–4 km al Poniente de La Parada, Servin 117 (CAS*, MEXU); Cuesta Colorada, km 21 de la carretera Vizarrón–Jalpán, Tenorio & Hernández 272 (CAS, ILL*, MO). San Luis Potosí. 5 km W of jct. of hwy. 86 with roads to Rayón and Cárdenas, 82 km W of Valles, Roe & Roe 2220 (NY*, WIS). Tamaulipas: ca. 5 km N of La Joya de Salas, trail to Carabanchel, Martin 129 (MICH*); 8 mi. E of Dulces Nombres, Meyer & Rogers 2640 (GH, MO*); 15 km al N de Tula, Puig 4741 (MEXU*).

8. Acacia durangensis (Britton & Rose) Jawad, Seigler & Ebinger, comb. nov. Basionym: Senegalia durangensis Britton & Rose, N. Amer. Fl. 23: 112. 1928. TYPE: Mexico. Durango: San Ramón, 21 Apr.–18 May 1906, E. Palmer 107 (holotype, NY*!, MEXU photo!; isotypes, F!, MO!, UC!, US!).

Shrub or small tree to 5 m tall with bark of main trunk dark gray, shallowly fissured; twigs light brown, not flexuous, puberulent; short shoots absent. Leaves alternate, 65–160 mm long; stipules herbaceous, light brown, narrowly triangular, to 2.5 \times 0.7 mm near the base, puberulent, persistent; petiole adaxially grooved, 30-50 mm long, puberulent and with erect hairs to 0.2 mm long; petiolar gland solitary, located near the middle of the petiole, sessile, elliptical, 1.1-2.2 mm across, apex irregularly raised, glabrous (Fig. 4A); rachis adaxially grooved, 50-130 mm long, puberulent and usually with minute purple glands, a sessile, flattened gland, 0.4-0.8 mm across, between the pinnae of the upper 1 to 2 pinna pairs; pinnae 6 to 13 pairs per leaf, 60-85 mm long, 8-14 mm between pinna pairs; petiolules 2.5-4.0 mm long; leaflets 28 to 36 pairs per pinna, opposite, 1.3-2.1 mm between leaflets, linear, $5.0-7.5 \times 1.3-2.1$ mm, loosely pubescent on both surfaces with appressed hairs, commonly purplish above, light green to purplish green beneath, lateral veins obvious with a midvein and 1 to 2 smaller veins from the base, base oblique, margins ciliate, apex obtuse to acute. Inflorescence a loosely flowered cylindrical spike 60-120 mm long, solitary (rarely 2) from the leaf axil, or rarely in short racemose clusters; peduncle $5-15 \times 1.0-1.8$ mm, puberulent; involucre absent; floral bracts linear, to 1 mm long, pubescent, early deciduous. Flowers sessile, creamy-white; calyx 5lobed, 1.0-1.4 mm long, densely appressed pubescent; corolla 5-lobed, 2.0-2.5 mm long, densely appressed pubescent; stamen filaments 5.5-7.5 mm long; ovary glabrous, on a stipe to 0.4 mm long. Legumes dark reddish brown, straight, flattened,

Representative specimens. MEXICO. Guanajuato:

Rancho Beltrán, 10 km al S de Xichú, Ventura & López 6778 (CAS, MEXU*). Hidalgo: Barranca de Tuzanapa, Zacualtipán, González 824 (MEXU*); Barrancas de Tolantongo, Cardonal, Hernández 3775 (MO*); 6 km al N de Zoquital, Hernández, Cortés & Hernández 6036 (CAS, MO*); a 3 km al N de Molanguito, Tolantongo, Cardonal, Medrano, Hiriart & Ortíz 10083 (MEXU*, MO); Sierra de la Mesa, Rose, Painter & Rose 9126 (GH, NY, US*). Nuevo León: a 24 km al S de Cd. Linares, Castillón 687 (MO, NY*); Cañon la Boca, camino a Cola de Caballo, Laguna de Sánchez, Villarreal, Carranza & Moreno 2736 (TEX*). Oaxaca: a 3 km sobre el camino Tamazulapán-Chilapa, Mendoza 930 (CAS, MO, MU*, WIS); a 4 km al SW de Tamazulapán, sobre la carretera Tamazulapán-Chilapa de Díaz, Rico, Torres & Cedillo 333 (CAS*, MO). Puebla: Barranca Honda al NW de Caltepec, Tenorio &

oblong, $80-120 \times 16-22$ mm, cartilaginous, transversely striate, glabrous to lightly puberulent, eglandular, dehiscent; stipe to 10 mm long; apex acuminate and usually beaked. Seeds not seen. Flowers: April-June.

Thorn-scrub forests and dry thick-Distribution. ets, 1600 to 2200 m elevation in the states of Durango and Chihuahua, Mexico (Fig. 3). Few specimens of Acacia durangensis are available for study; we saw the type and two others. This is the only species of this group known from Durango, and it occurs in a region that has been poorly collected. Superficially, A. durangensis is similar to A. mammifera, the leaflets being purplish above, light green beneath, with obvious veins and loosely pubescent on both surfaces with appressed hairs. Leaves with 6 to 13 pinna pairs, pinnae with 28 to 36 leaflets, and the sessile petiolar gland that is elliptical in outline and with a raised apex separate this taxon from A. mammifera. The petiolar gland is the most distinctive feature of A. durangensis. Other species of this group have a flat or doughnutshaped gland, or the gland is stalked. In A. durangensis, in contrast, the sessile gland appears as an elliptical mound, with a few indentations. On

dish yellow, exfoliating and papery; twigs light gray, becoming dark reddish purple, not flexuous, glabrous; short shoots absent. Leaves alternate, 30-400 mm long; stipules herbaceous, light brown, narrowly linear, 1.1×0.2 mm near the base, glabrous, tardily deciduous; petiole flattened, not grooved, 20-400 mm long, usually glabrous; petiolar gland solitary, located between to just below the lower pinna pair, sessile, circular, 0.3-0.7 mm across, doughnut-shaped, glabrous (Fig. 4G); rachis flattened, not grooved, 0-100 mm long, glabrous, glands absent; pinnae 1 (rarely 3) pair per leaf, 16-80 mm long; petiolules 2.5-8 mm long; leaflets 4 to 20 pairs per pinna, opposite, 1-5 mm distance between leaflets, oblong to elliptic, $3.0-7.5(12.0) \times$ 1.0-2.3 mm, glabrous to rarely lightly pubescent with appressed hairs on both surfaces, lateral veins not obvious with only one vein from the base, base oblique, margins lightly ciliate, apex narrowly acute to acuminate. Inflorescence a loosely flowered cylindrical spike 30-90 mm long, solitary from the leaf axil, or in short racemose clusters. Peduncle 5-25 \times 0.4-0.8 mm, glabrous or nearly so; involucre absent; floral bracts linear, to 1 mm long, glabrous to lightly pubescent, early deciduous. Flowers sessile, creamy-white; calyx 5-lobed, 1.3-2.2 mm long, glabrous; corolla 5-lobed, 2.4-3.6 mm long, glabrous; stamen filaments 6-8 mm long; ovary glabrous, on a stipe to 1 mm long. Legumes light yellowish brown, straight, flattened, oblong, 70-180 × 8-22 mm, chartaceous, irregularly striate, glabrous, eglandular, dehiscent; stipe to 14 mm long; apex obtuse. Seeds uniseriate, no pulp, dark brown, nearly circular, strongly flattened, 6-11 mm across, smooth; pleurogram usually absent, when present, U-shaped, about 2 mm across. Flowers: February-June.

herbarium specimens, this gland has a purple color, and rarely a few long hairs on its surface.

Though none were observed on the few specimens available, it is possible that plants of Acacia durangensis occasionally may have prickles. If present, this would suggest that A. durangensis is more closely related to A. macilenta and other members of the Acacia series Vulgares that commonly have prickles. Also, the petiolar gland of A. durangensis is similar to those found in many members of Acacia series Vulgares.

Representative specimens. MEXICO. Chihuahua: between El Tejebán and Río Unique, Bye, Davis, Randolph & Gerson 12774 (MEXU*). Durango: El Pino 20 km de el entronque a Sapioris, con la Brecha Coyotes-San Miguel de Cruces, Mpio. Tayoltita, 24°31'N, 105°49'W, Tenorio, Romero & Ramamoorthy 6323 (TEX*).

Distribution. Arid hills, rocky slopes and washes in desert scrub vegetation between sea level and 500 m elevation in Sonora, Mexico (Fig. 3). A common species at lower elevations in the

- 9. Acacia willardiana Rose, in Vasey & Rose, Contr. U.S. Natl. Herb. 1: 88. 1890. TYPE: Mexico. Sonora: rocky islands and ledges on the coast of Guaymas, 1–2 Apr. 1890, E. Palmer 164 (holotype, US!).
- Prosopis heterophylla Bentham, London J. Bot. 5: 82. 1846. Senegalia heterophylla (Bentham) Britton & Rose, N. Amer. Fl. 23: 114. 1928. TYPE: Mexico. Sonora: Alta, 1830, T. Coulter s.n. (holotype, TCD) [not Acacia heterophylla Willdenow, 1806].

Tree to 10 m tall with bark smooth, white to red-

state of Sonora, Acacia willardiana is a very obvious component of the desert scrub of this region because of it nearly white, to yellowish, to almost reddish, papery, exfoliating bark. Being so obvious, this species is commonly collected; numerous specimens are from the vicinity of Guaymas. The majority of the specimens lack pinnae, which are early deciduous; only the elongated, flattened petioles persist. Although flowering is common from February through May, it may occur at other times if moisture is available.

Acacia willardiana is easily separated from other members of this group. The most obvious differ-

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ences are the elongated, flattened petioles that may reach 400 mm in length, and the leaves with usually only one pair of pinnae, though rarely two or three may be present. This species has very small, tardily deciduous stipules (1.1 mm long or less), and the fruit valves are papery with more irregular striations than those found in other members of this group. The characteristic papery, exfoliating bark is shared only with *A. salazari*, a species of this group

Acad. Arts 21: 427. 1886. Senegalia millefolia (S. Watson) Britton & Rose, N. Amer. Fl. 23: 111. 1928. TYPE: Mexico. Chihuahua: Hacienda San José, near Batopilas, Aug. 1885, E. Palmer 45 (lectotype, designated by Isely (1969), GH!; isolectotypes, MEXU!, NY!).

Shrub or small tree to 3 m tall with bark gray, smooth when young, becoming fissured into square plates 1–2 cm across; twigs light brown to greenish brown, not flexuous, usually lightly puberulent; short shoots absent. Leaves alternate, 60-230 mm long; stipules herbaceous, light brown, narrowly linear, 6.5×0.5 mm near the base, usually glabrous, persistent; petiole adaxially grooved, 30-75 mm long, usually glabrous; petiolar gland absent; rachis adaxially grooved, 50-190 mm long, glabrous to lightly pubescent; a stalked gland with a globose apex, 0.3-0.9 mm across, between the pinnae of the upper 1 to 2 pinna pairs; pinnae (2)6 to 14 pairs per leaf, 30-55 mm long, 10-28 mm between pinna pairs; petiolules 2.0-4.0 mm long; leaflets 20 to 35(37) pairs per pinna, opposite, 0.8-1.6 mm between leaflets, oblong, 2.0–6.5 \times 0.7–1.4 mm, glabrous above, lightly pubescent beneath with appressed hairs, lateral veins not obvious with only one vein from the base, base oblique, margins sometimes ciliate, apex acuminate. Inflorescence a loosely flowered cylindrical spike 30-75 mm long, solitary (rarely 2 to 3), from the leaf axil; peduncle $5-15 \times 0.3-0.8$ mm, glabrous to lightly puberulent; involucre absent; floral bracts linear, to 1.3 mm long, glabrous to lightly pubescent, early deciduous. Flowers sessile, creamy-white; calyx 5lobed, 1.1-1.6 mm long, glabrous; corolla 5-lobed, 2.0-2.7 mm long, glabrous; stamen filaments 4.5-6.5 mm long; ovary glabrous, on a stipe to 0.4 mm long. Legumes light yellowish brown, straight, flattened, oblong, 70–170 \times 12–21 mm, chartaceous, irregularly striate, glabrous, eglandular, dehiscent; stipe to 12 mm, apex acute to obtuse. Seeds uniseriate, no pulp, dark brown, nearly circular, strongly flattened, 6.2-9.5 mm across, smooth; pleurogram U-shaped, 2-3 mm across. Flowers: June–August.

restricted to central Mexico.

Bentham (1846) tentatively assigned this taxon to *Prosopis heterophylla* based on a single fruiting specimen. He suggested that the general habit of the plant was more like that of *Prosopis* than any other genus, and mentioned the almost phyllodinous vertical expansion of the petiole. Based on flowering material, Vasey and Rose (1890) realized that this taxon was an *Acacia* and used the name *A. willardiana*, as Bentham's name was preoccupied.

Vassal (1972) noted that A. willardiana is a species with authentic phyllodes and suggested that, if he had seen flowering material, Bentham would have placed this species in the "Juliflorae." Vassal considered this species to be a member of his section *Heterophyllum*, subsection *Spiciferae*, and to have affinities to this predominantly Australian group. In our view, homology between the phyllodes of that group and the apparent petioles of A. willardiana should be examined more thoroughly. Further, in most other characteristics, this species differs little from other members of the A. coulteri group discussed in the present study.

Representative specimens. MEXICO. Sonora: rocky hill N of Guaymas, Blakley B-820 (ASU*); ¹/₂ mi. from top of microwave tower hill at Guaymas, Brunner 57 (ARIZ*); Bahía de San Carlos, ca. 24 km NW of Guaymas, Carter & Kellogg 3246 (SD*); ca. 1/2 mi. SW of Hotel Playa de Cortés, Miramar, Felger 5513 (ARIZ*); Isla Tiburón, Felger 9151B (ARIZ*, SD); Sierra Seri, Hast Eemla, Felger, Drees & Moser 74-8 (ARIZ*); Bahía Colorado, arroyo at E base of Morro Colorado, Felger & Hamilton 15638 (RSA*); Ensenada Grande, San Pedro Bay, Felger, Russell & Kleine 11588 (ARIZ, SD*); Sierra Bojihuacame SE of Cd. Obregón, Gentry 14483 (ARIZ*, US); 16 mi. S of Hermosillo, Gentry & Engard 551A (ASU*); 5 mi. N of Guaymas near hwy. 15, Henrickson 1565 (RSA*); Bahía San Carlos, Howard & Sphon s.n. (RSA*); Hermosillo, Jones 22495 (MO, POM*); microwave tower, 60 mi. N of Navijoa, Joseph s.n. (ARIZ*); hillside N of Guaymas, Knobloch 2325 (SD*); Guaymas, San Carlos Bay, road to Catch 22 beach, Landrum & Landrum 6315 (ASU*, MO, RSA); limestone quarry SE of Hermosillo, Martin s.n. (ARIZ*); Ardilla Island, Guaymas Harbor, Moran 4017 (SD*, US, WIS); rte. 15, ca. 25 mi. S of Hermosillo, Pinkava P12788 (ARIZ, ASU*); dry hillside slopes near Torres, Whitehead M250 (ARIZ*).

10. Acacia millefolia S. Watson, Proc. Amer.

Distribution. Desert grasslands, rocky slopes, subtropical scrub, and open oak woodlands from 700 to 1700 m elevation in southern Arizona, south through Sonora to western Chihuahua, Mexico (Fig. 3).

A shrub or small tree, mostly less than 3 m tall, *Acacia millefolia* is relatively common in desert grassland and desert scrub vegetation in extreme southern Arizona and adjacent Sonora, Mexico. Commonly collected along the steep sides and

floors of canyons, A. millefolia is rarely a dominant member of the vegetation, most collections indicating scattered individuals.

Though numerous specimens are available from throughout most of the geographic range of this taxon, no specimens, other than the type collection, are known from Chihuahua. This taxon may be extremely rare in southwestern Chihuahua, or it is possible that the collecting data on the type specimens are incorrect. This collection is more than 100 km east of any specimens of A. millefolia seen by the present authors. Acacia millefolia is distinct from other members of this group, as it lacks a petiolar gland and possesses a stalked rachis gland between the upper pairs of pinnae. The only other taxa of this group within the range of A. millefolia are A. willardiana and A. russelliana. Acacia millefolia is easily distinguished from A. willardiana, which has papery, exfoliating bark and leaves with only 1 to 3 pinna pairs. Leaflets with appressed hairs, the stalked rachis glands, and the persistent stipules of A. millefolia separate it from A. russelliana. In addition, A. millefolia is normally a shrub found above 700 m elevation, whereas the other species are usually trees and commonly occur at lower elevations.

23: 113. 1928. TYPE: Mexico. Michoacán: Xochiapa, 13 Apr. 1912, F. Salazar s.n. (ho-lotype, US!; isotypes, MEXU!, NY!).

Tree to 15 m tall with bark yellow to red or light gray, exfoliating and papery; twigs greenish brown to light reddish brown, not flexuous, usually glabrous; short shoots absent. Leaves alternate, 50-180 mm long; stipules herbaceous, light brown, narrowly linear, 4.5×0.6 mm near the base, glabrous, persistent; petiole adaxially grooved, 20-50(60) mm long, mostly glabrous; petiolar gland solitary, located between the lower pinna pair, sessile, nearly circular, 0.5-1.3 mm across, globose to doughnut-shaped, absent on most leaves; rachis adaxially grooved, 35-140 mm long, glabrous to lightly puberulent, a sessile, doughnut- to saucershaped gland, 0.5-1.0 mm across, between the pinnae of the upper 1 or 2(3) pinna pairs; pinnae 7 to 18 pairs per leaf, 35-63 mm long, 4-12 mm between pinna pairs; petiolules 2.4-4.0 mm long; leaflets 20 to 38 per pinna, opposite, 0.8-1.5 mm between leaflets, linear, $2.5-6.4 \times 0.9-1.3$ mm, usually lightly pubescent with appressed hairs beneath, commonly light greenish purple and glabrous above, lateral veins usually not obvious with only 1(2) vein(s) from the base, base oblique, margins usually ciliate, apex narrowly acute to acuminate. Inflorescence a loosely flowered, cylindrical spike 45–110 mm long, 1 to 3 from the leaf axil, or rarely in terminal racemose clusters; peduncle $5-10 \times 0.5-1.0$ mm, lightly puberulent; involucre absent; floral bracts linear, to 1 mm long, puberulent, early deciduous. Flowers sessile to rarely short stipitate, creamy-white; calyx 5-lobed, 1.5-2.3 mm long, lightly appressed pubescent; corolla 5-lobed, 2.5-3.5 mm long, lightly appressed pubescent; stamen filaments 4.5-7.0 mm long; ovary glabrous, on a stipe to 0.3 mm long. Legumes yellowish brown, straight, flattened, oblong, 115–180 \times 21–35 mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 13 mm long; apex obtuse. Seeds uniseriate, no pulp, dark reddish brown, circular to oblong, strongly flattened, $10.0-14.5 \times 7-$ 12 mm, smooth; pleurogram U-shaped, 1.2-3.0 mm across. Flowers: April-June.

Representative specimens. MEXICO. Sonora: 3 km by road S of Nacozari, Felger 3596 (ARIZ*, MICH, SD); 4 mi. N of Colonia Oaxaca, Hastings & Turner 65-25 (ARIZ, SD*); 5 mi. E of Mina Verde, Shreve 6753 (F*, MICH, MO); Río Bavispe, Colonia Oaxaca, White 679 (ARIZ*, GH, MICH); Cañon de Bavispe, White 3019 (ARIZ, GH, MICH*); 9 mi. W of La Angostura, White 4034 (ARIZ, GH, MICH*); Puerto del Molino Quemado, E of Colonia Morelos, White 4511 (ARIZ*, GH, MICH); 3 mi. S of Divisaderos, Wiggins 7457 (A, ARIZ, CH, F*, UC, US). U.S.A. Arizona: Cochise Co.: foothills of the Peloncillo Mts., T22S R32E S32, Kluever s.n. (ARIZ*). Pima Co.: Box Canyon, Santa Rita Mts., Goodding 89-53 (ARIZ*); Chimney Creek, Rincón Mts., Kearney & Peebles 10461 (ARIZ*, MICH, UC, US); Box Canyon, N end of Santa Rita Mts., McKeighen s.n. (ARIZ, ASU*, UC); 7 mi. W of hwy. 83 on Greaterville-Madera Canyon Road, Mc-Laughlin 64 (ARIZ*); vic. of Helvetia, Santa Rita Mts., Mittleman 373 (ARIZ, ASU*); Greaterville Road, 5.4 mi. W of hwy. 83, Pinkava, Keil & Lehto 14487 (ASU*); foothills of the Santa Rita Mts., Pringle s.n. (A, F, GH, MICH, NY*, US); Total Wreck Mines, Thornber 107 (MO, POM, UC*, US); Ophir Gulch, 4 mi. N and 2 mi. W of Sonoita, Tramontano T-25 (ARIZ*); Saguaro National Monument, Turner & Gunzel 78-111 (ARIZ*, SD). Santa Cruz Co.: about 3/4 mi. N of Sonoita Creek above Rio Rico, Kaiser 1394 (ARIZ*). New Mexico: Hidalgo Co.: about 0.5 mi. E of Arizona, about 50 m N of Mexico border, wedge Sec. 24 T24S, R22W, Spellenberg & Repass 5371 (NMC).

11. Acacia salazari (Britton & Rose) Lundell, Contr. Univ. Michigan Herb. 4: 8. 1940. Senegalia salazari Britton & Rose, N. Amer. Fl. Distribution. Thorn-scrub thickets, and disturbed dry forests from near sea level to 1800 m (but mostly above 1000 m) elevation in the states of Guererro, México, Michoacán, Morelos, Oaxaca, and Puebla, Mexico (Fig. 3).

A small tree, not exceeding 15 m in height, Acacia salazari is restricted to dry habitats, particularly thorn-scrub forests of southern Mexico. Many collections are from above 1000 m elevation, but a

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few individuals are reported from near sea level. Acacia salazari is similar to A. acatlensis with which it is sympatric nearly throughout its entire range. Both have leaves with many pinna pairs, and leaflets of similar size that are lightly pubescent with appressed hairs beneath and commonly light greenish purple and glabrous above. Acacia acatlensis, however, has minute purple glands along the petiole, rachis, and at the base of most leaflets; pinnae with more than 36 pairs of leaflets; petiolules that are mostly less than 2.0 mm long; and dark gray, fissured bark. Acacia salazari, in contrast, lacks the small purple gland and usually has fewer than 38 pairs of leaflets per pinna, petiolules that usually exceed 2.5 mm in length, and yellow to reddish bark that is papery and exfoliating. Some specimens with a mixture of characteristics of these two species suggest that they probably hybridize in Guerrero. Determination must await field studies. Although A. salazari is similar to other species of this group from southern Mexico, particularly A. centralis and A. usumacintensis, the papery, exfoliating bark allows for easy separation. Also, both of these species have pinnae with more than (36)40 leaflet pairs, whereas A. salazari has 38 or fewer leaflet pairs per pinna. Acacia usumacintensis has large, flattened petiolar glands that are located on the lower half of the petiole, while Acacia salazari commonly lacks petiolar glands. Occasionally, petiolar glands are found on a few leaves of some specimens; these are globose to doughnut-shaped, and located between the lower pair of pinnae. These glands are not common; most specimens lack petiolar glands altogether. On the remaining specimens, only one or two of the leaves have petiolar glands, and many are globose, not doughnut-shaped as is typical in most taxa of this group. Acacia salazari and A. millefolia are the only taxa in this group that usually lack petiolar glands.

MO*); a 3 km al E-NE de Teotitlán del Camino, carretera a Huautla, Sousa, Téllez, Germán & Rico 8079 (CAS*, TEX). **Puebla:** 20 mi. SE of Tehuacán on road to Teotitlán del Camino, Anderson & Anderson 5332 (MICH*); 3.5 km al N de Teotitlán, por el camino rumbo a Vigastepec, Cornelo 25 (MO*); Piaxtla, Huerta s.n. (NY*); just N of Coxcatlán along hwy. 131, Lavin, Sundberg, Hardison & Whittemore 4610 (TEX*); El Papayo, a 16 km al NW de Amatitlán, Sousa, Pérez & Ruiz 4339 (NY*); Ahuehuetilla, a 20 km al NW de Acatlán, Sousa, Téllez & Magallanes 5418 (MICH*, MO); hwy. 190, 17 mi. from the Oaxaca border in Puebla, Trott, Case, Thurm, Dunn, Hess & Dzie-

kanowski 140 (MO, NY*).

12. Acacia coulteri Bentham, in A. Gray, Pl. Wright. 1: 66. 1852. Senegalia coulteri (Bentham) Britton & Rose, N. Amer. Fl. 23: 112. 1928. TYPE: Mexico. Hidalgo: Zimapán, T. Coulter s.n. (holotype, K!, F photo!, GH photo!, MEXU photo!, MICH photo!, MO photo!, NY photo!, US photo and fragment!).

Shrub or small tree to 15 m tall with bark dark gray, shallowly furrowed; twigs light brown to greenish brown, not flexuous, glabrous to lightly appressed puberulent; short shoots absent. Leaves alternate, 50-150 mm long; stipules herbaceous, light brown, narrowly linear, 2.1×0.4 mm near the base, glabrous, tardily deciduous; petioles adaxially shallowly grooved, 25-55 mm long, usually lightly appressed puberulent; petiolar gland solitary, located on the upper third of the petiole and commonly just below the first pinna pair, sessile, nearly circular, 0.5-1.6 mm across, doughnutshaped, glabrous, rarely absent (Fig. 4E); rachis shallowly grooved adaxially, 20-100 mm long, lightly puberulent, a sessile, cup-shaped gland, 0.4-0.9 mm across, between upper pinna pair; pinnae 5 to 11 pairs per leaf, 40-90 mm long, 6-12 mm distance between pinna pairs; petiolules 3-5 mm long; leaflets 18 to 35 pairs per pinna, opposite, 1.5-2.3 mm interval between leaflets, oblong, $4.5-7.5 \times 1.4-2.1$ mm, glabrous above, lightly appressed pubescent beneath, lateral veins obvious with a midvein and occasionally one other vein from the base, base oblique, margins ciliate, apex broadly acute to obtuse. Inflorescence a loosely flowered cylindrical spike 50-90 mm long, 1 to 4 from the leaf axil, or rarely in terminal racemose clusters; peduncle 7–13 \times 0.5–1.0 mm, usually puberulent; involucre absent; floral bracts linear, to 1 mm long, puberulent, early deciduous. Flowers sessile, creamy-white; calyx 5-lobed, 1.2-1.6 mm long, lightly appressed pubescent; corolla 5-lobed, 1.9-2.6 mm long, lightly appressed pubescent; stamen filaments 5.0-6.5 mm long; ovary glabrous, on a stipe to 0.4 mm long. Legumes light yellowish brown to dark brown, straight, flattened, oblong,

Representative specimens. MEXICO. Guerrero: creek banks N of Chilpancingo, Clark 7235 (MO*); 21 km al NE de Chilpancingo, Delgado & García 1085 (CAS*, F, MEXU, MO, NY, WIS); a 20 km al N de Chilpancingo, camino a Iguala, Martínez 557 (F*); N de Zumpango del Río, Rico & Funk 204 (CAS*); 24 km al N de Zumpango del Río hacia Iguala, Torres, Tenorio & Romero 1243 (CAS*, MO). México: El Jumate, a 1 km al S después del cruzero San Antonio del Rosario, Rico & Martínez 848 (NY*). Michoacán: between Río Tepalcatepec and Arteaga, McVaugh 22520 (CAS, MICH*, MO, NY); en Las Cañas, cerca de la desviación al Infiernillo, carretera Nueva Italia-Playa Azul, Soto 1081 (CAS, MO*); carretera Nueva Italia-Arteaga, Soto & Aureolea 7745 (MEXU*). Morelos: yard, Apuyeca, Clausen 6036 (CU*). Oaxaca: Rancho El Mezquite, a 7 km al S de Teotitlán, Sousa 6934 (CAS, MO, SD, UC*); Teotitlán del Camino, en la orilla del Pueblo, Sousa, Téllez, Germán & Rico 8060 (CAS,

 $100-185 \times 16-25$ mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 15 mm long; apex acute to acuminate. Seeds uniseriate, no pulp, dark reddish brown, circular to nearly oblong, strongly flattened, 7.3-10.5 \times 5.5-8.5 mm, smooth; pleurogram U-shaped, 2.2-3.5 mm across. Flowers: April-August.

Distribution. Open dry forest, dense thornscrub thickets, and dry rocky slopes below 1800 m

Liga, Ventura & López 8935 (MEXU*). Hidalgo: 10 km al NW de Zimapán, González 2358 (DS, LL, MICH*). Nuevo León: jungles, N of Linares, Clark 6819 (MO*); El Cercado, Santiago, Hinton 24102 (NY*, TEX); Sierra de la Silla, Pringle 2549 (A*, CM, F, G, GH, MO, NY, PH, UC, US, VT, WIS); N slope of La Silla, White & Chatters 8 (GH, MICH*, TEX). Querétaro: 15 km al SE de Agua Zarca, Rubio 1675 (MICH*, MO, TEX, WIS). San Luis Potosí: 10 mi. W of Tamuin on the Tampico-Valles hwy., Crutchfield & Johnston 5401 (MICH*, TEX); Minas de San Rafael, Purpus 5181 (F*, G, GH, MO, NY, UC, US); 16 km W of Tamuin, Seigler, Clarke & Potgieter 13010 (EIU*, ILL). Tamaulipas: Ejido Los Angeles, Diaz, Cedilla & Jiménez 484 (MEXU*); Camino a la mina El Berrinche, Victoria, Jiménez 67 (MEXU*); 60 mi. N of Victoria, Hitchcock & Stanford 6867 (CU, DS, F, GH, ILL*, ISC, MO, NY, UC, US); along route 70 about 3 mi. S of Victoria, King 4498 (F, MICH, NY, TEX*, UC, US); 2 km WNW of Gómez Farías, Martin 71C (MICH, VT*); Puerto de la Angostura, km 658-60 between Victoria and Mante, Moore, Jr. & Wood, Jr. 3629 (A*, BH, MICH, UC); Victoria, Nilson 4421 (GH, NY, US*); 33 mi. N of Mante, Seigler, Richardson & Thompson 11627 (EIU*, ILL).

elevation in the foothills and mountains of northeastern Mexico in the states of Coahuila, Guanajuato, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, and Tamaulipas (Fig. 3).

Abundant in northeastern Mexico, Acacia coulteri is a common component of relatively dry forests and thorn-scrub thickets. Many of the collections are from roadsides and rocky pastures. This taxon is abundant in the states of Tamaulipas and San Luis Potosí, becoming less common to the south. Acacia coulteri is similar morphologically to A. russelliana, which is common in Sonora and parts of Sinaloa. Acacia russelliana is usually a small shrub or understory tree that rarely exceeds 4 m in height. Acacia russelliana has usually been considered as conspecific with A. coulteri, Britton and Rose (1928) being the only authors that recognized the two as distinct. Both of these taxa have leaves with fewer than 12 pinna pairs, pinnae with fewer than 35 leaflet pairs, petiolules that exceed 2.4 mm in length, and identical petiolar glands. Though similar in many traits, these taxa are easy to separate, A. coulteri having appressed pubescence on the lower leaflet surface, perianth, and the rachis and pinna rachises; A. russelliana, in contrast, being glabrous throughout. The stipules of Acacia coulteri seedlings are decidedly spinescent, but are only weakly rigid after the first leaf stage, and become progressively smaller and less rigid on older plants (Vassal, 1972). Because this species lacks prickles and because of correlations of the cotyledonary petiole and shape, as well as certain other features, Vassal placed A. coulteri in his subgenus Acacia, a group roughly equivalent to Bentham's (1842) Acacia series Gummiferae. However, A. coulteri differs in some significant features from members of that series. Chief among them, the pollen grains of A. coulteri are porate, whereas those of other members of Bentham's series Gummiferae are colporate (Vassal, 1972).

13. Acacia russelliana (Britton & Rose) Lundell, Contr. Univ. Michigan Herb. 4: 7. 1940. Senegalia russelliana Britton & Rose, N. Amer. Fl. 23: 112. 1928. TYPE: Mexico. Sinaloa: vicinity of San Blas, 22 Mar. 1910, J. N. Rose, P. C. Standley & P. G. Russell 13204 (holotype,

US!; isotype, GH!, NY!).

Shrub or small tree to 8 m tall with bark dark gray, shallowly furrowed; twigs light brown to greenish brown, not flexuous, glabrous; short shoots absent. Leaves alternate, 60–140 mm long; stipules herbaceous, light brown, narrowly linear, to $2.5 \times$ 0.4 mm near the base, glabrous, tardily deciduous; petiole adaxially shallowly grooved, 20-50 mm long, glabrous; petiolar gland solitary, located near the middle of the petiole to just below the lowest pinna pair, sessile, usually circular, 0.4-1.5 mm across, doughnut- to urn-shaped, glabrous, sometimes absent; rachis shallowly grooved adaxially, 30-90 mm long, glabrous, rarely a sessile, doughnut-shaped gland, 0.4-0.9 mm across, between the upper pinna pair; pinnae (2)4 to 11 pairs per leaf, 35-70 mm long, 5-12 mm between pinna pairs; petiolules 2.0-3.5 mm long; leaflets 18 to 34 pairs per pinna, opposite, 0.9-1.8 mm distance between leaflets, oblong, $4.0-7.5 \times 1.3-1.8$ mm, glabrous, lateral veins obvious with a midvein and 1 to 3 smaller veins from the base, base oblique, margins sometimes lightly ciliate, apex obtuse to broadly acute. Inflorescence a loosely flowered cylindrical spike 25-60 mm long, solitary (rarely 2 to 3) from the leaf axil, or rarely in terminal racemose clusters; peduncle 1–10 \times 0.4–0.7 mm, glabrous; involucre absent; floral bracts linear, to 1 mm long,

Representative specimens. MEXICO. Coahuila: Cañon el Puerto, Sierra de Santa Rosa, Villarreal, Vásquez, Gutíerrez & Urbina 5958 (TEX*). Guanajuato: between Aurora and Xichu, McVaugh 14866 (MICH*); Mina de La

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glabrous, early deciduous. Flowers sessile, creamywhite; calyx 5-lobed, 1.0-1.4 mm long, glabrous; corolla 5-lobed, 1.7–2.5 mm long, glabrous; stamen filaments 5–7 mm long; ovary glabrous, on a stipe 2–3 mm long. Legumes greenish brown to dark brown, straight, flattened, oblong, 55–170 \times 16– 27 mm, cartilaginous, transversely striate, glabrous, eglandular, dehiscent; stipe to 15 mm long, apex acute to obtuse, sometimes beaked. Seeds uniseriate, no pulp, reddish brown, circular to oval, strongly flattened, $6.8-9.6 \times 5.1-8.0$ mm, smooth; pleurogram U-shaped, 2–3 mm across. Flowers: March-August.

tively widely spaced. The proposed hybrid is similar to A. russelliana in having stipules to 2.5 mm long, petioles that are round in cross section and slightly adaxially grooved, a doughnut-shaped petiolar gland, and leaves with 2 to 11 pairs of pinnae. Few specimens are available for study [Gentry 14337 (MICH, US), Gentry 14420 (LL, MICH, US), Gibson & Gibson 2101 (ARIZ, ASU), Rose, Standley & Russell 13317 (US)]; field studies will be necessary to determine the status of these specimens.

Distribution. Dry, deciduous, tropical forests to thorn-scrub and desert-scrub vegetation, mostly on rocky slopes, from near sea level to about 700 m elevation in southwestern Sonora, and extreme northern Sinaloa, Mexico (Fig. 3).

A small shrub or understory tree not exceeding 8 m in height, Acacia russelliana is a common species of Sonora and parts of Sinaloa. Occurring at elevations below 700 m, it appears to be a common component of desert and thorn-scrub vegetation, and is also found as an understory tree in tropical deciduous forests.

Britton and Rose (1928) were the first to recognize this taxon, all previous and subsequent authors considering it to be conspecific with Acacia coulteri, a species of northeastern Mexico. It is easily distinguished from this taxon by being essentially glabrous; A. coulteri, in contrast, has leaves that are lightly pubescent beneath with appressed hairs, and the petiole and rachis are lightly puberulent, as are many other vegetative parts of the plant. Also, the perianth of most flowers of A. coulteri is puberulent, but it is glabrous in A. russelliana. The only acacia species of this group found within the range of Acacia russelliana are A. willardiana and A. millefolia. Both taxa are easily separated from A. russelliana; A. willardiana by its extremely long, flattened petioles topped with 1 to 3 pairs of pinnae, and A. millefolia by the stalked gland with a bulbous apex between the upper pinna pair, the long, usually persistent stipules, and the missing petiolar gland. It is quite probable that Acacia russelliana occasionally hybridizes with A. willardiana in thornscrub forests on the arid, rocky slopes at lower elevation in extreme northern Sinaloa, Mexico. The few specimens available suggest that the probable hybrid is similar to A. willardiana in being a small tree with exfoliating, papery bark, petioles that commonly exceed 100 mm in length, and pinnae with fewer than 26 pairs of leaflets that are rela-

Representative specimens. MEXICO. Sinaloa: vicinity of Culiacán, Brandegee s.n. (GH*, UC); Cerros de Navachiste about Bahía Topolobampo, Gentry 14309 (US*); Cerros del Fuerte, 18-24 mi. N of Los Mochis, Gentry 17635 (LL*); near Yacht Hotel Topolobampo, Hastings & Turner 64-103 (SD*); vicinity of Culiacán, Rose, Standley & Russell 14994 (US*). Sonora: 34 km E of Hermosillo on road to Sahuaripa, Felger, Aronson & Shmida 84-204 (SD, TEX*); foothills at S end of Sierra Libre, 12.3 mi. S of La Palma on hwy. 15, Felger & Reichenbacher 85-1084 (TEX*); SW of Ures, Felger 3000 (ARIZ, LL*); Río Sonora, 22.2 mi. by road E of Mex. 15 on road to Ures, Felger 3628 (ARIZ*); Lake Mocuzari, Johnson 191-77 (CAS*); Cerro Prieto, 8.6 mi. E of Navajoa, Sanders, Guzy, Way, Charlton & McIntosh 4618 (NY*, TEX); summit of Cerro Prieto, 15 km E of Navajoa, Sanders, Ballmer, Charlton, Clarke & Mayor 9286 (SD*), Río Mayo area, 9 mi. NW of Alamos, Sanders, Ballmer, Charlton, Clarke & Mayor 9440 (SD*, TEX); Navajoa, summit of Cerro Masiaca, Sanders, Devender, Devender, Meyer & Pitzer 12767 (CAS*, MO, TEX, WIS); Alamos, Cerro La Luna, Sanders, Friedman, Spenger & Kossack 13260 (CAS*, MO, TEX); at crossing of Río Sonora, 23 mi. NE of El Sacatón, 19 Sep 1934, Shreve 6703 (GH*, MICH, MO); Cerro Prieto, 15 km al E de Navajoa, Tenorio, Romero, Ignacio & Davila 10202 (F, CAS, MO, NY*); near the Mirador, Alamos, Devender & Lindquist 94-828 (NY*); crossing the Río Sonora, 13 mi. S of Ures, Wiggins 7320 (A, DS, F, MICH, UC, US*); 15 mi. S of La Palma, between Hermosillo and Guaymas, Wiggins & Rollins 228 (A, LL, DS*, MICH, MO, NY, UC).

Literature Cited

- Barneby, R. C. & J. W. Grimes. 1996. Silk Tree, Guanacaste, Monkey's Earring. Mem. New York Bot. Gard. Vol. 74, Part 1.
- Bentham, G. 1842. Notes on Mimoseae, with a synopsis of species. London J. Bot. 1: 318-392, 494-528.

——. 1846. Notes on Mimoseae, with a synopsis of species. London J. Bot. 5: 75-108.

———. 1875. Revision of the order Mimoseae. Trans. Linn. Soc. London 30: 335-664.

- Britton, N. L. & J. N. Rose. 1928. Mimosaceae. North American Flora 23(2): 1–194.
- Chappill, J. A. & B. R. Maslin. 1995. A phylogenetic assessment of tribe Acacieae. Pp. 77-99 in M. Crisp & J. J. Doyle (editors), Advances in Legume Systematics 7: Phylogeny. Royal Botanic Gardens, Kew.

Clarke, H. D. 1995. Systematics and evolutionary studies of Acacia series Gummiferae (Fabaceae: Mimosoideae). Ph.D. Dissertation, Department of Plant Biology, University of Illinois, Urbana-Champaign.

-, D. S. Seigler & J. E. Ebinger. 1989. Acacia far-

nesiana (Fabaceae: Mimosoideae) and related species from Mexico, the southwestern U. S., and the Caribbean. Syst. Bot. 14: 549-564.

, —_____& _____. 1990. Acacia constricta (Fabaceae: Mimosoideae) and related species from the southwestern U.S. and Mexico. Amer. J. Bot. 77: 305– 315.

- Conn, E. E., D. S. Seigler, B. R. Maslin & J. Dunn. 1989. Cyanogenesis in Acacia subgenus Aculeiferum. Phytochemistry 28: 817–820.
- Feigl, F. & V. A. Anger. 1966. Replacement of benzidine by copper ethylacetoacetate and tetra base as spot-test reagent for hydrogen cyanide and cyanogen. Analyst 91: 282–284.

(NTSYS-pc), Version 1.70, Applied Biostatistics, Setauket, New York.

- Seigler, D. S. & J. E. Ebinger. 1988. Acacia macracantha, A. pennatula, and A. cochliacantha (Fabaceae: Mimosoideae) species complexes in Mexico. Syst. Bot. 13: 7– 15.
 - —— & ——. 1995. Taxonomic revision of the antacacias (Fabaceae, Mimosoideae, Acacia, series Gummiferae) of the New World. Ann. Missouri Bot. Gard. 82: 117–138.

_____, J. E. Dunn, E. E. Conn & G. L. Holstein. 1978. Acacipetalin from six species of *Acacia* of Mexico and

- Isely, D. 1969. Legumes of the United States: I. Native Acacia. SIDA 3: 365-386.
- Maslin, B. R. & C. H. Stirton. 1997. Generic and infrageneric classification in *Acacia* (Leguminosae: Mimosoideae): A list of critical species on which to build a comparative data set. Bull. Groupe Int. Étude Mimosoideae. 20: 22–44.
- Pedley, L. 1978. A revision of *Acacia* Mill. in Queensland. Austrobaileya 1: 75–234.
- Rico A., L. & A. Rodríguez. 1998. Mimosaceae R. Br. Tribu Acacieae Benth. Fascículo 20. Flora del Valle de Tehuacán-Cuicatlán. Instituto de Biología, UNAM, México D.F.

- Texas. Phytochemistry 17: 445-446.
- Sokal, R. R. & F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California.
- Standley, P. C. 1920. Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. 23: 1–1721.
- Tantisewie, B., H. W. L. Ruijgrok & R. Hegnauer. 1969.
 Die Verbreitung der Blausäure bei den Cormophyten.
 5. Mitteilung: Über cyanogene Verbindungen bei den Parietales und bei eingen weiteren Sippen. Pharmaceutisch Weekblad voor Nederland 104: 1341–1354.
- Thompson, R. L. 1980. A Revision of the Genus Lysiloma (Leguminosae). Ph.D. Dissertation, Department of Botany, Southern Illinois University at Carbondale, Illinois.
 Vasey, G. & J. N. Rose. 1890. List of plants collected by Dr. Edward Palmer in Lower California and western Mexico in 1890. Contr. U.S. Natl. Herb. 1: 63–90.
- Vassal, J. 1972. Apport des recherches ontogéniques et seminologiques à l'étude morphologique, taxonomique et phylogénique du genre Acacia. Bull. Soc. Hist. Nat. Toulouse 108: 105–247.
- Willdenow, C. L. 1806. Species Plantarum. Berlin. (Aca-

Rohlf, F. J. 1993. Numerical Taxonomy Systems-pc

cia) 4 (2): 1049 - 1093.